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CORRIGENDA

Vol. xvi. P. 381, 6th line from bottom, *for* "curly kale" *read* "cabbage," and in 3rd line from bottom *for* "cabbage" *read* "curly kale."

Vol. xvi. P. 382, the subtitles of Tables XV and XVI should be interchanged.

Vol. xvii. P. 11, line 3, *for* "cross-fertilisation in height" *read* "self-fertilisation in height."

WILLIAM BATESON

1861–1926

ὁ ἀνεξέταστος βίος οὐ βιωτὸς ἀνθρώπῳ

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THE INHERITANCE OF WING COLOUR AND PATTERN IN THE LEPIDOPTEROUS GENUS *TEPHROSIA* (*ECTROPIS*). II. EXPERIMENTS INVOLVING MELANIC *TEPHROSIA BISTORTATA* AND TYPICAL *T. CREPUSCULARIA*.

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I. INTRODUCTORY.

IN previous work (Harrison 1920, 1923) on the inheritance of melanism in hybrids between *Tephrosia crepuscularia* Bkh. and *T. bistortata* Goeze the melanism has invariably been introduced by means of the melanic variety *delamerensis* of the former species. On the contrary, in the present set of experiments, equally concerned with hybrids between these two species, the melanism originated with *T. bistortata.*

As the relationship between *T. crepuscularia* (the Small Engrailed) and *T. bistortata* (the Engrailed) has already been discussed at some length in the two papers to which reference has just been made, and further details supplied in a recent paper (Harrison and Peacock 1925) no description of these forms or of the variety *delamerensis* is necessary here. However, a brief account of the origin and appearance of the black *bistortata* must be supplied for, instead of being a wild race like *T. crepuscularia* var. *delamerensis*, it is an artificial product developed from a typical Kentish[1] strain removed to Birtley, Co. Durham, in 1921 and inbred there for five successive generations. Throughout that period it was reared about one hundred yards from a road on which practically every lepidopterous species is melanic or melanochroic to a greater or less degree; in addition, the food supplied was uniformly smoke-contaminated hawthorn gathered from the hedges along the road in question. As the result of such treatment, in spring 1923, a single melanic female was reared from which the melanic strain was built up. Complete details

[1] Similar success attended efforts to induce melanism in a Hampshire-Cleveland strain, but melanic *bistortata* of such origin were not introduced into the present series of experiments.

of this experiment, with an exhaustive account of subsequent work on the inheritance of the induced melanism within the limits of the species *T. bistortata*, have been given elsewhere (Harrison and Garrett 1926).

These melanic *bistortata* are extreme in their coloration for head, thorax, abdomen and wings (save for the usual narrow, pale, subterminal band characterising the wings of so many melanic Boarmiinae) can only be described as being coal-black. In this respect they contrast greatly with the melanic form of the closely allied *T. crepuscularia*, for only rarely is the melanin present in that species in such quantities as to warrant the *delamerensis* form being described as other than grey or dark grey. This difference was scarcely to be anticipated in view of the relationship existing between the two insects, but it supplies one more proof, if that were required, of their specific distinctness.

Much more remarkable than the colour differences is the fact that, whilst the melanism in *T. crepuscularia* behaves as a simple Mendelian dominant and remains so, with certain peculiarities to be mentioned immediately, when *delamerensis* is crossed with *T. bistortata*, in *bistortata* the melanism is recessive. This occurrence was quite unexpected, for melanism in the Boarmiinae in all the species[1] hitherto investigated has proved to be a dominant character.

The curious point in the interspecific crosses is the circumstance that in certain F_2 individuals the melanism seems to degenerate into a permanent mosaic, itself dominant to type.

Hence the questions to be answered in the present research were three in number:

(1) Does the artificial melanism of *T. bistortata* when brought into crosses with *T. crepuscularia* (type) still behave as a recessive?

(2) Does it break down under the same circumstances like the melanism of *T. crepuscularia* var. *delamerensis*?

(3) If so, how is the new character inherited?

II. The Experiments.

The type *crepuscularia* employed were, as usual, derived from a Kentish source whilst the *bistortata* with which they were crossed, whether typical or melanic, were selected from the F_3 brood 24 *b*[2], resulting from pairing the original black female with a typical male.

[1] In addition to work already published by Onslow (1919, 1920 *a*, 1920 *b*) and by myself (1920, 1923) I have shown experimentally, in work to be published shortly, that melanism in *Boarmia repandata* and *B. gemmaria* is likewise dominant.

[2] This brood label is that used in the 1926 paper, *q.v.*

To be exact, the actual parents of this F_3 lot were a type F_2 female and one of its black brothers. As this F_3 brood comprised 36 types and 36 melanics it is clear that its female parent had been heterozygous for melanism, and that therefore the 36 types were in the same condition.

Although the insects to be crossed belonged to different species no difficulty was encountered in bringing about the desired reciprocal matings, and in all cases large batches of eggs, in no respect inferior in fertility to those of the pure species, secured.

As the tiny larvae emerged they were placed on newly expanded hawthorn leaves procured from an area free from smoke deposits. This food was replaced in the later larval instars by seedling knotgrass (*Polygonum aviculare*). They did well, and in the end the large broods, set out with all pertinent details in respect to sex and colour in Tables I–IV, were reared.

But before presenting these tables certain important facts must be stated in connection with the emergence of these broods. Without exception, the *bistortata* ♀ × *crepuscularia* ♂ batches yielded males only which appeared in one continuous stream from 3 May until the first week in November, by far the greater portion emerging after 2 June. Unlike these lots, those representing the reciprocal cross included the two sexes in approximately equal numbers but with the females anticipating the males in their *éclosion*. Thus up to 1 June, of brood *B* (an enormous batch) there had emerged 89 ♀♀ and 18 ♂♂; after that date the emergences were 33 ♀♀ and 86 ♂♂. In the same way, prior to 8 June brood D_1 had yielded 55 ♀♀ and 7 ♂♂; later 9 ♀♀ and 57 ♂♂ appeared. Since the strain of *crepuscularia* used was univoltine and that of *bistortata* bivoltine, there exists here, to assess it at its least value, a distinct hint that the inheritance of voltinism may be sex-linked in its nature.

TABLE I.

Homozygous black bistortata ♀ × *homozygous type* crepuscularia ♂.

$tt \times TT$

	Types			
Family	Females	Males	Total	Melanics
A_1	0	68	68	None
A_2	0	91	91	None, but see below
A_3	0	37	37	None
A_4	0	63	63	None
A_5	0	84	84	None
		Totals	343	0
		Expectation ...	343	0

TABLE II.

Homozygous type crepuscularia ♀ × *homozygous black* bistortata ♂.

$TT \times tt$

Family	Types: Females	Males	Total	Melanics
B_1	121	105	226	None
B_2	101	94	195	None, but see below
B_3	60	54	114	None, but see below
B_4	77	71	148	None, but see below
B_5	62	60	122	None
B_6	46	40	86	None
	Totals ...	...	891	0
	Expectation ...		891	0

TABLE III.

Heterozygous type bistortata ♀ × *homozygous type* crepuscularia ♂.

$Tt \times TT$

Family	Types: Females	Males	Total	Melanics
C_1	0	53	53	None
C_2	0	58	58	None
C_3	0	74	74	None
	Totals ...	...	185	0
	Expectation	...	185	0

TABLE IV.

Homozygous type crepuscularia ♀ × *heterozygous type* bistortata ♂.

$TT \times Tt$

Family	Types: Females	Males	Total	Melanics
D_1	64	64	128	None
D_2	55	51	106	None
D_3	49	46	95	None
	Totals ...	...	329	0
	Expectation	...	329	0

As will be perceived at once, these tables present no melanics of either sex, and the evidence they supply strongly supports the view that, as in the intraspecific *bistortata* tests, melanism is comporting itself as a Mendelian recessive. Nevertheless, there is a distinct suggestion offered by the presence of certain nondescript individuals in broods A_2 (one ♂), B_2 (one ♀ and one ♂), B_3 (one ♂), and B_4 (one ♂) that, exactly as in the earlier interspecific work, with melanic *crepuscularia* and typical *bis-tortata*, in certain cases degradation changes take place in the determiner

for melanism. However, this important difference must be emphasised that, whilst the breaking up of the *crepuscularia* melanism reveals itself in F_2 broods, here it is manifested in the F_1 lot. Hence the circumstances are not the same, and direct experiment is necessary before we can determine whether we are dealing with cases of somatic segregation or genetic changes equivalent to those described in the 1923 paper.

With the exception of the male in B_2 all the affected individuals resemble the low grade mosaics of the F_2 *crepuscularia* ♀ × *bistortata* ♂ hybrids. On the other hand, the B_2 male possesses an entirely black left forewing, whilst the corresponding lower wing is of a mosaic facies higher in the scale than those just considered. If this specimen is contrasted with the mosaics studied in 1923, when not a single specimen displayed a wing entirely melanic, the opinion is forced upon that, almost certainly, the correct explanation of the condition is somatic segregation.

In addition to these noteworthy insects certain males, otherwise typical, when fresh from the pupa, show irregularities in the normal ground colour[1] of that sex for distinctly paler areas, sometimes large in extent, are discernible.

Obviously, no further tests were possible within the limits of broods A_1, A_2, A_3, A_4, A_5, A_6, C_1, C_2, and C_3, but utilising (1) males from these batches, (2) both sexes of the reciprocal cross, (3) melanic *bistortata* and (4) homozygous and heterozygous type *bistortata*, every type of mating likely to throw light on the research was made. Furthermore, the mosaic female from B_2 was paired with a typical brother, and the similar male from B_4 with a type female from B_3.

The outcome of these matings in the matters of sex and colour may be determined from Tables V–XI.

TABLE V.

F_2 *broods bred from type* crepuscularia ♀ × *black* bistortata ♂.
$Tt \times Tt$

	Types			Melanics		
	Females	Males	Total	Females	Males	Total
F_2B_1	24	28	52	8	9	17
F_2B_4	31	38	69	10	11	21
F_2B_5	43	45	88	12	16	28
F_2B_5	25	28	53	9	9	18
F_2B_6	16	21	37	5	7	12
	Totals ...	...	299			96
	Expectation	...	296·25			98·75

[1] Both parent species are sexually dimorphic, the dimorphism being strong in *bistortata* and less obvious in *crepuscularia*; in the hybrid it is exaggerated.

TABLE VI.

F_2 *broods bred by mating the males of the cross* bistortata ♀ × crepuscularia ♂ *with females of the reciprocal cross, the original* bistortata *in both cases being melanic.*

$Tt \times Tt$

Family	Types			Melanics		
	Females	Males	Total	Females	Males	Total
B_1♀ × A_1♂	9	19	28	2	7	9
B_2♀ × A_1♂	20	46	66	7	13	20
B_4♀ × A_2♂	15	32	47	5	11	16
	Totals ...	...	141			45
	Expectation	...	139·5			46·5

TABLE VII.

Backcrosses involving F_1 crepuscularia ♀ (*type*) × bistortata ♂ (*black*) *and homozygous black* bistortata.

$Tt \times tt$

Fam.	Origin of family	Types			Melanics		
		Females	Males	Total	Females	Males	Total
a	B_2♀ × *bist.*♂	48	53	101	44	51	95
b	*bist.*♀ × B_3♂	8	21	29	8	20	28
c	*bist.*♀ × B_4♂	13	28	41	14	30	44
d	B_4♀ × *bist.*♂	36	40	76	37	37	74
		Totals ...	...	247	—	—	241
		Expectation	...	244	—	—	244

TABLE VIII.

Backcrosses involving F_1 crepuscularia ♀ (*type*) × bistortata ♂ (*black*) *and heterozygous type* bistortata.

$Tt \times Tt$

Fam.	Origin of family	Types			Melanics		
		Females	Males	Total	Females	Males	Total
e	B_1♀ × *bist.*♂	40	42	82	12	15	27
f	B_1♀ × *bist.*♂	30	39	69	10	12	22
g	B_3♀ × *bist.*♂	31	30	61	8	11	19
h	*bist.*♀ × B_4♂	25	47	72	7	16	23
i	*bist.*♀ × B_4♂	4	10	14	1	4	5
		Totals ...	...	298	—	—	96
		Expectation	...	295·5	—	—	98·5

TABLE IX.

Backcrosses involving F_1 bistortata ♀ (*black*) × crepuscularia ♂ (*type*) *and melanic* bistortata.

$tt \times Tt$

Fam.	Origin of family	Types: Females	Types: Males	Types: Total	Melanics: Females	Melanics: Males	Melanics: Total
j	*bist.* ♀ × A_1 ♂	12	27	39	13	23	36
k	*bist.* ♀ × A_1 ♂	19	39	58	19	38	57
l	*bist.* ♀ × A_4 ♂	9	15	24	6	16	22
m	*bist.* ♀ × A_5 ♂	11	36	47	15	27	42
		Totals ...	...	168	—	—	157
		Expectation	...	162·5	—	—	162·5

TABLE X.

Backcrosses involving F_1 crepuscularia ♀ (*type*) × bistortata ♂ (*black*) *and homozygous type* bistortata.

$TT \times Tt$

Family	Origin of family	Types: Females	Types: Males	Types: Total	Melanics
n	*bist.* ♀ × B_2 ♂	25	52	77	None
o	B_2 ♀ × *bist.* ♂	40	44	84	None
p	B_3 ♀ × *bist.* ♂	44	47	91	None
q	B_5 ♀ × *bist.* ♂	16	17	33	None
		Totals ...	...	285	0
		Expectation	...	285	0

TABLE XI.

F_2 *crosses involving the streaked insects from the* F_1 *lots* B_2 *and* B_3.

Family	Types: Females	Types: Males	Types: Total	Melanics: Females	Melanics: Males	Melanics: Total
Mosaic ♀ B_2 × Type B_2 ♂	32	44	76	13	12	25
Type B_3 ♀ × Mosaic B_4 ♂	30	31	61	8	12	20
Totals			137	—	—	45
Expectation if we are dealing with a case of somatic segregation...			136·5	—	—	45·5

The facts included in the preceding set of tables can only lead to the conclusion that melanism brought into *crepuscularia-bistortata* crosses *viâ* the species *bistortata* remains, as within the species, a simple Mendelian recessive. Moreover, we learn that the F_1 mosaics differ in no respect genetically from their typical brothers and sisters, for the ratios obtained in the F_2 broods from such insects, as set out in Table XI, are of the

usual 3 : 1 type. "Mosaic," therefore, in these hybrids, unlike the similar phenomenon in the F_2 *crepuscularia* var. *delamerensis* ♀ × *bistortata* ♂ hybrids, has no germinal basis and depends solely on somatic segregation.

Only one further point needs emphasis and that is that, throughout these tables, wherever we are dealing with back crosses between the F_1 hybrid males and *bistortata* females, the sex ratio uniformly becomes 1 ♀ : 2 ♂♂; on the other hand, when, in similar cases, *bistortata* supplies the male the sex ratio remains normal. These facts are intimately bound up with the non-viability of the females in the original F_1 *bistortata* ♀ × *crepuscularia* ♂ batches and are in complete harmony with the results of all similar experiments, whether carried out with typical or with melanic insects of these two species.

III. Summary.

(1) In interspecific crosses between *Tephrosia crepuscularia* and *T. bistortata* melanism introduced by *T. bistortata* remains, as within the limits of the species, a Mendelian recessive.

(2) In certain F_1 broods mosaics appeared; their appearance was shown to depend on somatic segregation.

(3) In the F_1 batches resulting from crossing *bistortata* females and *crepuscularia* males the females are non-viable.

(4) Similarly, in back crosses between *bistortata* females and the two possible F_1 males, one half of the females die.

(5) No disturbances of the sex ratio arise in the *crepuscularia* ♀ × *bistortata* ♂ broods.

In conclusion I have to thank my friend Mr J. R. Johnson of Gateshead for attending to my larvae and pupae when I was absent in Canada, and also to acknowledge the receipt of a grant of £20 from the Armstrong College Research Endowment Fund Committee to assist this and other researches.

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SELF AND CROSS-FERTILISATION IN *LOLIUM PERENNE* L.

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Introduction.

In his work on *Cross and Self-fertilisation in Plants*, Darwin[1] included *Phalaris canariensis* and *Zea Mays*. In each case, plants obtained by cross-fertilisation exceeded those obtained by cross-fertilisation in height, both during growth and at maturity.

Zea Mays has been extensively studied in this connection by more recent workers, and for this species similar conclusions have been reached[2].

Kirk[3] has found that Red Clover behaves in the same way, while McRostie[4] obtained similar results with the Sunflower. He, however, found that in Timothy (*Phleum pratense*) "self-fertilisation does not seem to be accompanied by any decrease in vigour of the inbred progeny," but although he quotes cases he gives no figures in support of this statement.

Material and Methods.

In 1921 the present writer selected from amongst various populations, plants of *Lolium perenne*, which, from an economic standpoint, appeared to be promising, and in 1922 many of these were crossed by hand, while at the same time inflorescences of the same plants were isolated for self-pollination and fertilisation. Unfortunately, a number of these plants proved to be highly self-sterile so that only in a few cases was a fair quantity of selfed seed obtained.

[1] Third edition, London, 1891, p. 233.

[2] See for instance East, E. M. and Jones, D. F. *Inbreeding and Outbreeding*, London, Lippincott Co. 1919; Jones, D. F. "The productiveness of Single and Double First Generation Corn Hybrids," *Am. Jour. Agron.* Vol. xiv. p. 241; and "Methods of Seed Corn Production being Revised," *Jour. Heredity*, Vol. xv. p. 291.

[3] Kirk, L. E. "Artificial Self-Pollination of Red Clover," *Sci. Agriculture*, Vol. v. p. 179.

[4] McRostie, G. P. "Some Forage Crop Needs and Difficulties in Canada," *Sci. Agriculture*, Vol. v. p. 97.

The seed obtained by both methods was germinated early in 1923, sterilised soil being used in order that no volunteer seedlings should be included in the experiment. The seedlings were planted out in permanent positions in April in short rows of ten plants—each plant being allowed sufficient space for full development. As far as could be judged, the ground was very uniform, and since the lots were in any case small, no great distance separated any of them from others. In order to obtain the best possible comparison between L_1[1] and F_1 progeny from the same parent, however, such lots were arranged to occupy adjacent positions.

During 1923 all lots were uniformly treated, several level cuts being made so as to prevent seed-setting and to encourage even establishment of the plants.

After a preliminary level cut in February the first cut of the experiment proper was taken on 19 March, 1924, and the green produce of each plant was weighed independently. For further cuts the lots were divided into two sections, "A" and "B." The plants in each section were approximately or exactly equal in number (see Table II). The plants for each section were taken serially so that in a lot of twenty plants the first ten would form the "A" section.

The "A" plants in each lot were again cut on 7 April, 5 May, 19 May, 16 June, 14 July and 11 August. Aggregate weights only were determined for 7 April and 14 July, and the average weight per plant calculated.

Section "B" was treated in exactly the same way, except that the plants were not cut on 7 April and 5 May.

The "A" sections were in each case therefore cut seven times in the course of the season, while the "B" sections were cut five times.

Discussion of Results.

Comparison of productivity in L_1 *and* F_1 *families.* In comparing the average productivity of L_1 and F_1 families the fact that the lots were divided into "A" and "B" sections can be ignored since the plants in each section were approximately equal in numbers. Even when the results of the two sections are taken together, it will be seen from Table I that the number of plants in some families was small, but since the difference between L_1 and F_1 is so well marked, this fact probably does not materially affect the comparisons to be made.

[1] L_1 is the symbol used at the Welsh Plant Breeding Station to indicate first generation line progeny. Thus when plant *bA* 50 is self-pollinated, the next generation so obtained is the L_1 of *bA* 50, and bears the reference number 50 *bA* (1). One of these L_1 plants again self-pollinated would give the L_2 and so on.

TABLE I.

Average green weight per plant in various L_1 *and* F_1 *families.*

Station Number	Parents	Generation	No. of plants	Average wt. gms.	Relative weights L_1	Relative weights F_1
70 *bA* (1)	*bA* 70	L_1	6	203	—	—
99 *bA* (1)	*bA* 70 × *bA* 69	F_1	30	406	100	253
69 *bA* (1)	*bA* 69	L_1	7	118	—	—
101 *bA* (1)	*bA* 69 × *bA* 50	F_1	4	382*	100	172
50 *bA* (1)	*bA* 50	L_1	14	330	—	—
61 *bA* (1)	*bA* 61	L_1	39	167	—	—
114 *bA* (1)	*bA* 61 × *bA* 83	F_1	34	329	100	244
83 *bA* (1)	*bA* 83	L_1	21	103	—	—
89 *bA* (1)	*bA* 83 × *bA* 80	F_1	8	295	100	286
57 *bA* (1)	*bA* 57	L_1	10	107	—	—
90 *bA* (1)	*bA* 57 × *bA* 80	F_1	30	347	100	324
91 + 95 *bA* (1)	*bA* 69 × *bA* 80	F_1	19	258	100	219
94 *bA* (1)	*bA* 80 × *bA* 69	F_1	20	317	100	269
92 *bA* (1)	*bA* 70 × *bA* 80	F_1	20	281	100	138
98 *bA* (1)	*bA* 75 × *bA* 69	F_1	12	354	100	300
100 *bA* (1)	*bA* 64 × *bA* 69	F_1	3	329*	100	279
102 *bA* (1)	*bA* 45 × *bA* 69	F_1	18	291	100	247
104 *bA* (1)	*bA* 76 × *bA* 69	F_1	17	331	100	281
48 *bA* (1)	*bA* 48	L_1	14	238	—	—
112 *bA* (1)	*bA* 48 × *bA* 43	F_1	30	327	100	137

* In both these cases, only "A" plants were available. This means that they are at a slight disadvantage as compared with other lots.

Only in the case of three F_1 families were corresponding L_1 families of both parents obtained, so that only in these cases is a full comparison possible. In these three cases, the average for the two L_1 families is compared with the corresponding F_1 family, while in the others the F_1 can only be compared with the L_1 of one of the two parents. In Table I such comparisons are made on the basis $L_1 = 100$.

In two of the cases where a full comparison is possible, the F_1 exceeded the L_1 by well over 100 per cent., while in the third case, the L_1 and F_1 compare as 100 : 172. Thus in all three cases, the F_1 has proved to be by far the more productive.

Where a one-sided comparison only is possible, the F_1 exceeds the L_1 by anything from 37 to 224 per cent., so that the results are in full agreement with those given by the double comparisons.

It may also be mentioned that although L_1 families of *bA* 80 and *bA* 43 did not come into the experiment, these two plants were not completely self-sterile. The very few plants to which each gave rise when self-fertilised were, however, extremely poor, so that even if a sufficient number of plants for inclusion in the experiment had been obtained, they would have widened rather than narrowed the difference between L_1 and F_1.

It will be noted from the table that some L_1 families, particularly 50 *bA* (1) and 48 *bA* (1), have given relatively good results, so that it is evident that in *Lolium perenne* occasional plants can be found which produce relatively vigorous progeny from self-fertilisation. Even when these are crossed with plants which produce inferior L_1 progeny, however, the resulting F_1 is distinctly superior even to the best L_1.

Total productivity of F_1 *families.* In Table II various F_1 families are arranged according to the order in which they were planted in the garden. The intervening L_1 families are not included in the Table, but since in many cases there was no L_1 family corresponding to the F_1, a number of the latter drills actually occupied adjacent positions as shown in the table. In any case, adjacent lots in the table were only separated by a few feet and since the ground was apparently very uniform[1], total productivity can perhaps be legitimately compared.

TABLE II.

Results for various F_1 *families.*

Station Number	Parents	"A" results: No. of plants	"A" results: Aver. gn. wt.	"B" results: No. of plants	"B" results: Aver. gn. wt.	Aver. for "A" and "B"	Relative wts. average of "A" and "B" plants: A	Relative wts. average of "A" and "B" plants: B
88 *bA* (1)	*bA* 64 × *bA* 80	10	278	11	287	282	100	103
90 *bA* (1)	*bA* 57 × *bA* 80	15	340	15	354	347	100	104
91 *bA* (1)	*bA* 69 × *bA* 80	8	236	8	288	262	100	122
92 *bA* (1)	*bA* 70 × *bA* 80	10	258	10	303	281	100	117
94 *bA* (1)	*bA* 80 × *bA* 69	10	288	10	346	317	100	120
97 *bA* (1)	*bA* 75 × *bA* 80	15	225	15	248	237	100	110
98 *bA* (1)	*bA* 75 × *bA* 69	6	325	6	383	354	100	118
99 *bA* (1)	*bA* 70 × *bA* 69	15	313	15	499	406	100	159
100 *bA* (1)	*bA* 64 × *bA* 69	3	329	—	—	—	—	—
101 *bA* (1)	*bA* 69 × *bA* 50	4	382	—	—	—	—	—
102 *bA* (1)	*bA* 45 × *bA* 69	9	269	9	313	291	100	116
104 *bA* (1)	*bA* 76 × *bA* 69	10	325	7	353	331	100	109
105 *bA* (1)	*bA* 76 × *bA* 45	15	275	13	317	296	100	115
109 *bA* (1)	*bA* 64 × *bA* 57	14	296	14	457	377	100	154
110 *bA* (1)	*bA* 64 × *bA* 43	15	276	15	386	332	100	140
112 *bA* (1)	*bA* 48 × *bA* 43	15	269	15	384	327	100	143

For this purpose, the average for the "A" and "B" sections can again be taken. The outstanding lots appear to be 90 *bA* (1), 94 *bA* (1), 98 *bA* (1), 99 *bA* (1), 104 *bA* (1) and 109 *bA* (1).

Both crosses into which plant *bA* 57 has entered have given particularly good results, and while this plant has interacted well with both *bA* 80 and *bA* 64, these two when intercrossed gave relatively poor

[1] It is probable that families 98, 99, 101 and 102 *bA* (1) were slightly favoured by position.

results. Plant *bA* 69, particularly when crossed with *bA* 75, *bA* 70 or *bA* 76 gave very good results, but neither this nor *bA* 76 was sufficiently dominating to give good results when crossed with *bA* 45.

It would therefore appear that F_1 results vary quite distinctly according to parentage, and that some plants have a marked superiority for use as parents.

The response of various F_1 *families to different systems of treatment.* Aggregate results for *Lolium perenne* have shown that seasonal productivity is profoundly affected by the system of cutting adopted[1]. Plants cut at short intervals throughout the growing season give a smaller total produce than when some of the early cuts are omitted.

For this reason, and in order to test the response of the several families to each method of cutting, as such, the present families were, as already explained, divided into two sections, two of the early cuts being omitted in the case of section "B."

In Table II, the results for each section are given separately, and the relative weights are shown by expressing the "A" results as 100 in each case and the "B" results proportionately.

In every case the drills cut on the "B" method have given the highest yields, but the relative increase over the drills cut more frequently varies greatly in the different families. Thus while in family 88 *bA* (1) the advantage in favour of the "B" system only amounts to 3 per cent., in family 99 *bA* (1) it reaches 59 per cent.

These comparisons are both interesting and significant when considered in relation to parentage. Thus when *bA* 80 was crossed either with *bA* 57 or *bA* 64 the result was all but identical in spite of the fact that cross *bA* 57 × *bA* 80 was distinctly the superior in total productivity. In each case the increased yield resulting from reducing the number of cuts early in the season was very small.

On the other hand, when *bA* 64 and *bA* 57 were themselves intercrossed, the F_1 plants were greatly favoured by the omission of two of the early cuts.

Almost exactly parallel results were obtained when *bA* 69, *bA* 70 and *bA* 80 were intercrossed, although in these cases there was a somewhat greater response in favour of the "B" system in the crosses involving *bA* 80.

In none of the families in which plant *bA* 80 was used as one of the parents was there a great response to the "B" system of cutting, and this plant would appear to have a dominating influence against such

[1] *Bulletin Series H.* No. 3, Welsh Plant Breeding Station, Aberystwyth, pp. 32 *et seq.*

response. This influence is, however, less potent in some crosses than in others.

From the results for families 99 *bA* (1) and 109 *bA* (1) it is evident that plants *bA* 57, *bA* 64, *bA* 69 and *bA* 70, have no such influence, since these two families have responded well to the omission of early cuts.

That *bA* 80 and *bA* 69 are different in their action is further shown by the results obtained when each in its turn is crossed with *bA* 70 and with *bA* 75. In each cross into which *bA* 69 entered the response was greater although *bA* 75 itself appears to be similar to *bA* 80 in its influence.

Summary.

The seasonal productivity of *Lolium perenne* plants obtained by self- and by cross-fertilisation have been studied. The results show that cross-fertilisation gives an increase in productivity ranging from 37 to 224 per cent.

A comparison of F_1 families with each other suggests that certain plants are far more valuable than others for use as parents when total productivity is mainly considered.

That the omission of some of the early cuts generally makes for a higher total yield in a particular season is strongly supported, but it is evident that all F_1 families do not respond equally to such treatment. Some plants appear to have a dominating influence against such response although they do not at the same time necessarily reduce total productivity. A number of plants when not subjected to this parental influence give progeny which respond readily to such a system of cutting. Such families may give an increased yield of over 50 per cent., even when only two of the early cuts are omitted.

From the economic standpoint, these results are obviously important. Self-sterility is one of the greatest obstacles in the way of the improvement of grasses, but even where, as in *Lolium perenne*, this is very pronounced, occasional plants are found which are relatively highly self-fertile. Owing to lack of vigour in the selfed progeny of many promising types, however, it is probable that it will be difficult to use these to the extent and in the manner that would seem desirable. At the same time, such plants when intercrossed may give very vigorous F_1 families.

In this respect, certain crosses are more valuable than others, and by a system of intercrossing it would seem possible to eliminate plants which prove to be but poor parents.

When types adapted to suit a particular set of economic conditions are sought it is necessary to estimate productivity on a basis which corresponds as nearly as possible to those conditions in order that the criterion adopted may be a correct guide to selection. The evidence brought forward indicates that some crosses give rise to families which suffer but to a small extent by frequent and continuous cutting, while other families give far better results when early cuts are omitted. Evidence obtained in connection with extensive trials now in progress at the Station would suggest that the two systems of cutting under review may be taken roughly to correspond with continuous grazing and with hay conditions respectively. Consequently by the adoption of the methods of comparison indicated it should be possible to select plants for use as parents in the production of either desired type.

SEX-LINKAGE AND OTHER GENETICAL PHENOMENA IN CANARIES.

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(With one Coloured Plate.)

In 1908, in collaboration with Miss Marryat, I published a preliminary note on the Inheritance of Sex in Canaries in Report IV of the Evolution Committee of the Royal Society. Since that date the experiments were continued by me till the year 1915, when, on account of the war, the work had to be laid aside.

The lapse of time that has occurred, and the fact that my attention has been occupied with problems of a very different nature, have, I fear, caused me to lose touch with the work, and I can but offer the results of my experiments with due apology for the many shortcomings which they exhibit. At the same time I wish to place them on record, in the hope that, inadequate as they are, they may prove of some interest and use to other workers in the same field. Some of these experiments were carried out at Cambridge, but from 1910 onwards the work was transferred to the John Innes Horticultural Institution. The experiments were assisted by a grant from the Royal Society.

The experiments on sex-linkage are chiefly of interest as providing evidence of the occasional appearance of the unexpected terms; namely, black-eyed *females* from the cross black-eyed ♀ × pink-eyed ♂, and on two occasions a pink-eyed *male* from the same mating. Exceptional occurrences of this kind have been encountered in the descent of sex-linked characteristics, especially in *Drosophila*. They may be interpreted as the consequence of non-disjunction, following the classical examples discovered by Bridges. But the possibility of crossing-over as a source of the abnormality cannot be excluded, when, as in the present examples, cytological evidence has not been obtained. The purpose of this publication is simply to make available the observed facts without attempting an interpretation.

The experiments with Lizard canaries, in addition to their bearing on the problem of sex-linkage, give some slight indications as to the genetical behaviour of the peculiar features characteristic of the Lizard.

Various crosses designed to give evidence as to the nature and origin

of the varieties of the canary were in contemplation. Of these the only one which had already led to a positive result was the crossing of the canary with *Chrysomitris cucullata*, the Venezuelan Siskin, which produced a *fertile* hybrid. In view of the accepted history that canaries all descend from *Serinus canarius* and the well-recognised fact that hybrids between canaries and numerous species of finches are sterile (with very doubtful exceptions) this new observation is of considerable importance.

A recapitulation of the facts already known to canary fanciers may not be out of place as a preliminary to the record of the experiments.

The cinnamon canary, when mated with other varieties, gives certain curious results. The cinnamon canary is so called on account of the colour of its plumage, which is brownish in tint, due to the presence of a chocolate melanin and the absence of black melanin. The green canary has both pigments present in its feathers.

When the cinnamon canary is first hatched the eye looks pink, whereas in ordinary canaries the eye of the newly hatched bird looks black. When the cinnamon canary is older the eye looks dark, so that in the adult bird it is extremely difficult, if not impossible, to distinguish the colour of its eye from that of the common canary by inspection. Microscopical examination, however, reveals the fact that the pigment of the cinnamon differs from the normal eye in being chocolate only. All birds with black in their feathers have black in their eyes.

The yellow birds, having no melanins present in the plumage, may be either cinnamon or black-eyed birds.

To avoid ambiguity the cinnamons will be referred to as *pink-eyed*, the other varieties as *black-eyed*.

The pink-eye is a Mendelian recessive and the offspring of two pink-eyed birds is always pink-eyed.

When pink-eyed and black-eyed birds are bred together, the fanciers are agreed that the results are as follows:

1. PE hen and BE cock gives all young of both sexes BE.

2. BE hen and PE cock will give all *male* offspring BE. The female young are most commonly PE; *BE hens may occur*, but the PE young are always hens.

I may further preface my account by stating that canary breeding is beset with many difficulties. The young cannot feed themselves when first hatched. The use of an incubator is, therefore, out of the question, and hand-feeding with large numbers is out of the range of practical

politics. It is impossible to predict whether a hen will prove a good mother or no, and the caprices of hen canaries are many. In some cases a hen will not sit unless the cock is left with her, in others she will only sit when the cock has been removed. Some hens will refuse to feed. Sometimes when the cock is left with the hen, he will interfere and not allow the hen to carry out her duties towards her young. Consequently very many young birds do not survive the nest. Whenever possible, however, the sex of the young was determined, but occasionally this was not possible as even a good mother may so crush and trample on the young as to make dissection of the corpse later on impossible. Moreover, more than once I had the misfortune to get mice into the breeding room, and the best canary hen in the world will not carry out her duties properly in such adverse circumstances.

In this account I propose to deal with the results of the matings between BE birds and PE birds and of the heterozygous birds resulting from these unions with regard to sex and colour of the offspring.

Black-eyed hens and pink-eyed cocks.

Taking the results of all the years and pooling them together, there were in all 470 young as follows:.

BE ♀s	BE ♂s	PE ♀s	PE ♂s
21	203	234	2

and in addition 5 BE birds and 5 PE birds hatched which could not be sexed. There were, therefore, 229 BE birds to 241 PE birds, the PE birds being in excess. Expectation would give 235 of each sort. There were 255 ♀s and 205 ♂s which could be sexed, and here the females are in excess of the males.

If sex-linkage were complete and no disturbance occurred we should expect no PE cocks and no BE hens. With the latter as an abnormality the fanciers, as already mentioned, are acquainted. The still rarer PE cocks might easily be overlooked. Both, however, certainly appear occasionally from this mating, though whether the numerical proportions are significant cannot be declared, and still less can we decide the question of their genetical causation.

1. I will deal with the case of the PE cock first. These two cocks appeared in separate nests. The first one hatched was the offspring of a BE hen bought in 1909, having been hatched in 1908. This hen, 191 A, was mated in 1909 with a PE cock and produced 4 young; 1 BE cock and 3 pink-eyed ♀s, all of which died before leaving the nest. The

following year, 1910, she was mated with heterozygous BE cocks and produced in three nests 4 cocks, all BE, 1 BE hen and 1 PE hen. The 4 cocks all lived to maturity, the hens died in the nest.

In 1911 she was mated with a PE cock, No. 279, and she had by him 3 nests. In the first nest of this season she had 1 BE ♂, 1 PE ♂ and 1 PE ♀. In the second nest she had 2 BE ♂s and 2 PE ♀s. In the third nest only 1 egg was fertile and gave a PE ♀. None of the young lived to maturity; the PE cock lived 7 days only.

191 A was a bad mother as will be seen from her record. Out of 18 young only 4 birds were reared. No further nests could be taken from her as she died the following spring just before the breeding season. It may be worth noting here that she produced ♂s and ♀s in equal numbers; taking the results of all her nests there were 9 hens and 9 cocks. The PE cock No. 279 was further mated to 2 other BE hens.

No. 208, by whom he had 3 BE ♂s and 2 PE ♀s.

No. 246, by whom he had 5 BE ♂s.

He died in 1913, so no further use could be made of him.

The second case of the PE cock appearing as a result of the mating of BE hen and PE cock occurred in 1914. The mother was No. 482 and was a first-year bird from a mating of PE ♀ × BE ♂ (heterozygous). She was not related in any way to 191 A ♀ or 279 ♂. She was mated to a PE ♂, No. 491, also a first-year bird. The grandparents of 491 were a BE hen, No. 202 (bought), and a PE ♂ (bought). They produced No. 402 PE ♀ and No. 400 BE ♂, who were the parents of No. 491, so that this cock was inbred. 482 ♀ and 491 ♂ had two nests.

In nest 1 there were 3 eggs, 1 infertile and 2 fertile, which, on hatching, gave 1 PE ♂ and 1 PE ♀. In the second nest there were also only 3 eggs, of which only 1 hatched, giving a BE ♂. Total 3 birds; 1 PE ♂, 1 BE ♂. The PE ♂ lived long enough to get his feathers and then died.

♂ 491 was mated also with another BE ♀, No. 332, a three-year old hen, by whom he had 1 BE ♀, 1 BE ♂ and 2 PE hens.

He died the same year, so that even if war conditions had not made it impossible to continue the experiments, no further matings could have been made between 482 ♀ and 491 ♂.

It will be seen from the results that PE cocks can be produced by the mating of BE hens and PE cocks, but that their appearance is very rare, which may account for the fanciers having missed them. It so happened that in both cases in which they appeared in my breeding room the birds survived for some time. Also, as I have already stated,

I always ascertained the sex of the young when possible. But it must be remembered that the fancier does not do this, and it is quite possible, therefore, that the appearance of PE cocks from this mating may have been overlooked for this reason. If the PE cock appears rarely and is not likely to survive the nest or the dangers of the first moult, the fact of his presence among the offspring would escape attention.

2. The total number of BE hens produced in the matings between BE hens and PE cocks was 21. These 21 hens were produced by 15 hens; 6 of these were from my own breeding, the rest were from stock bought from time to time.

I used for the matings of BE hens and PE cocks 82 hens in all and 48 cocks as mates, so that only 18·3 per cent. of the hens used produced BE hens. I have no information as to how this result compares with the results obtained by other canary breeders.

I wanted, if possible, to raise up a stock of hens bred in this way, so that an attempt could be made to analyse their genetic characters.

The difficulties which beset the path of the canary breeder prevented me from carrying out my purpose. Not only did I have to contend with the obstacles, already referred to in the introduction, but also, it so happened that for three years in succession no BE hen appeared as a result of these matings. Thus this part of the experiment must be counted as a failure.

In analysing the results of these matings I propose to enter into considerable detail.

TABLE I.

BE ♀ × PE ♂	BE ♀	BE ♂	PE ♀
25 × 24	1	3	3
13 × 24	2	1	4
141 × 127	1	1	3
142 × 124	1	—	1
170 × 93	1	1	1
170 × 222	1	1	3
141 × 222	1	1	—
210 × 185	1	3	6
204 × 231	1	—	1
152 × 61	1	—	2
316 × 302	2	2	1
332 × 422	1	—	—
332 × 451	1	1	2
456 × 488	1	1	1
496 × 448	1	—	1
497 × 469	1	2	—
500 × 523	1	1	2
521 × 532	2	1	—
	21	19	31

First is given in Table I the results of the matings in which the BE hens appear, followed by an account of the ancestry as far as known of the birds concerned.

This will be followed by Table II (p. 26), in which are given the results of all the matings of each hen, including the mating which gave the BE hens.

In Table III (p. 26) all the matings of the cocks, including the matings which gave the BE hens, are given.

In this table the proportion of hens to cocks is approximately 3–1.

Hens 170, 456, 496, 497, 500, 521 were of my own breeding. Of these hens 170, 497, 500 and 521 are all related to one another, being all descended from the mating 13 ♀ × 24 ♂, which gave BE hens when mated together.

BE ♀ 13 × 24 PE ♂

BE ♀ 36   37 PE ♀ × 7 BE ♂

BE ♀ *170*   172 BE ♂ × 191 A BE ♀

BE♀ 328 × 262 BE ♂   BE ♀ 316 × 263 BE ♂

BE ♀ 209 × 277 PE ♂

PE ♀ 406 × 350 BE ♂   BE ♀ 428 × 418 BE ♂

**497* BE ♀   **500* BE ♀

BE ♀ 249 × 172 BE ♂

BE ♀ 242 × 292 BE ♂   PE ♀ 337 × 298 BE ♂

BE ♀ 340 × 347 BE ♂

521 BE ♀

* Hens 497 and 500 are also descended from ♀ 191 A, which, as has already been stated, produced a PE ♂ when mated with a PE ♂.

Hen 456 is descended from hen 332, which, as will be seen on reference to Table I, produced BE hens when mated with ♂s 422 and 491, both PE. She is also related to hen 496 through the PE ♀ 286, which appears in the ancestry of both.

PE ♀ 308 × 333 BE ♂

BE ♀ 332 × 277 PE ♂ — 298 BE ♂ × 286 PE ♀ × 362 BE ♂

PE ♀ 382 × 353 BE ♂ — *496* BE ♀

456 BE ♀

N.B.—The ♂ 277 also occurs in the table of descent of hen 500.

Of the cocks in the mating 8 were of my own breeding, viz. Nos. 93, 422, 491, *488*, 448, *469*, 523 and *532*. Of these cocks Nos. 93 and 422 are not related to any of the other birds, whether ♀s or ♂s occurring in these matings, or to each other. ♂s 488, 532 and 469 are all descended on the father's side from the mating of ♀ 13 × 24 ♂, the father being ♂ 263. They are thus related to hens 170, 497, 500 and 521. ♂ 448 is descended from ♂ 277 and is thus related to hens 456 and 500.

Finally cocks 491 and 523 are related together.

302 PE ♂ × 202 BE ♀ × 278 PE ♂ — PE ♀ 334 × 323 BE ♂

PE ♀ 402 × BE ♂ 400 — PE ♀ 40 × 352 BE ♂

491 PE ♂ — 523 PE ♂

Cocks 491 and 523 are related through hen 202 to hen 497, which gave a BE hen when mated with cock 469 (see Table I). The mother of hen 497 is hen 406, own sister to hen 407, the mother of 523 ♂.

Thus it will be seen that a certain amount of relationship can be traced between various of the cocks and hens whose numbers occur in Table I. Unfortunately there is not enough evidence to show that this relationship has any bearing one way or the other on the results obtained. I was only able to breed from two F_1 ♀s, Nos. 36 and 51, out of BE ♀ 13 × PE ♂ 24.

♀ 36 × 46 ♂ (F_1 out of BE ♀ × PE ♂) gave 1 PE ♀ and 1 BE ♂.
× 77 ♂ PE gave 1 PE ♀ and 1 BE ♂.
× 59 ♂ PE gave 3 PE ♀s and 2 BE ♂s.
♀ 51 × 15 ♂ PE gave 2 PE ♀s and 1 BE ♂.
× 45 (BE ♂ ex BE ♀ × PE ♂) gave 1 BE hen and 1 BE ♂.

From Table II, therefore, the proportion of hens to cocks is approximately 2–1, instead of 3–1 as in Table I.

I have not considered it necessary to enumerate all the hens used, since there is nothing to be said about them beyond what has already been stated in the case of the mating producing the PE cock.

TABLE II.

Showing all the matings of each hen mentioned in Table I.

BE ♀ × PE ♂	BE ♀	BE ♂	PE ♀
25 × 24	1	3	3
× 59	—	1	1
13 × 24	2	1	4
141 × 127	1	1	3
× 222	1	1	—
× 231	—	1	1
142 × 124	1	—	1
170 × 93	1	1	1
× 186	—	3	1
× 126	—	1	2
× 222	1	1	3
152 × 61	1	—	2
210 × 185	1	3	6
204 × 231	1	—	1
× 186	—	—	1
316 × 302	2	2	1
× 126	—	4	1
× 277	—	2	1
332 × 422	1	—	—
× 491	1	1	2
× 278	—	2	2
× 277	—	—	4
456 × 488	1	1	1
× 399	—	2	1
496 × 447	—	1	2
× 488	1	—	1
500 × 523	1	1	2
521 × 532	2	1	—
497 × 469	1	2	—
	21	36	48

TABLE III.

PE ♂	No. of matings with BE ♀s	BE ♀	BE ♂	PE ♀	PE ♂
24	7	3	11	15	—
127	3	1	3	6	—
124	2	1	1	1	—
93	1	1	1	1	—
222	4	2	3	4	—
185	5	1	8	13	—
231	5	1	1	6	—
61	2	1	3	4	—
302	8	2	11	10	—
422	1	1	—	—	—
491	2	1	2	3	1
488	1	1	1	1	—
448	2	1	1	3	—
469	2	1	2	1	—
523	1	1	1	2	—
532	3	2	5	2	—
		21	54	72	1

Taking now the results of mating F_1 birds (ex BE ♀ × PE ♂) with PE cocks we have:

F_1	BE ♀	BE ♂	PE ♀
BE (out of BE × PE) × PE	—	4	6
BE (out of PE × BE) × PE	2	23	39
	2	27	45

That is 47 ♀s–27 ♂s, and instead of equality of colour 29 BE's–45 PE's.

We have still to consider the result of mating the same hens, that produced BE hens in the mating BE ♀ × PE ♂, with heterozygous BE cocks, but before doing this, it will be better to take first the results of this mating BE hen and BE heterozygous cock as a whole.

If the BE hen be always heterozygous, and such a thing as a homozygous BE hen be an impossibility, then the mating between BE hen and BE heterozygous cocks should produce a proportion of 3 BE to 1 PE. Also if the fanciers' view, that the PE cocks cannot result from the union of BE hen and PE cock be correct, it should also be impossible to get PE cocks from the mating of BE hen and BE heterozygous cocks.

From my experiments I find that pooling all the results together I got from BE hen and BE heterozygous cock:

BE ♀s	BE ♂s	PE ♀s	PE ♂s
125	158	120	3

(There were also 4 BE and 4 PE birds which could not be sexed.)

Thus there were 287 BE birds to 127 PE birds. The expectation would be 310·5 BE to 103·5 PE. Instead of equality in the sexes we have 245 ♀s to 161 ♂s.

TABLE IV.

♀ ♂	BE ♀	BE ♂	PE ♀	
13 × 46 (out of PE × BE)	—	2	1	
× 48 („ PE × BE)	2	1	—	
25 × 84 („ BE × PE)	2	1	—	
× 104 („ PE × BE)	1	1	1	
141 × 47 („ PE × BE)	—	1	2	
× 172 („ PE × BE)	—	—	1	
170 × 176 („ PE × F_1 BE)	2	2	1	
204 × 102 („ PE × BE)	1	1	—	
× 172 („ PE × BE)	—	—	2	
× 264 („ BE × F_1 BE)	3	1	1	
316 × 263 („ BE × F_1 BE)	1	3	—	
496 × 440 („ BE × F_1 BE)	—	1	1	
500 × 472 („ BE × F_1 BE)	1	1	—	and one PE not sexed
	13	15	10	

It will be more convenient to deal with the cases in which the PE cocks appear, after considering the matings of BE hens (which have given BE hens from the matings BE ♀ × PE ♂) with BE heterozygous cocks.

Eight of these hens were used in the matings, Nos. 13, 25, 141, 170, 204, 316, 496 and 500. In Table IV are given the matings and their results.

These hens, therefore, when mated with heterozygous cocks do not apparently show any peculiarity of behaviour, differing from those already recorded.

I used for the mating of BE hen and heterozygous BE cock, 91 hens and 69 cocks in all. Of these 91 hens 23 were of my own breeding and all the cocks used were bred by me.

Dealing first with the hens of unknown origin, the results of matings between these hens and F_1 cocks out of BE hens and PE cocks gave

51 BE ♀s, 49 BE ♂s, 30 PE ♀s, 2 PE ♂s.

Matings between hens of unknown origin × F_1 cocks out of PE hens × BE cocks gave

22 BE ♀s, 32 BE ♂s, 33 PE ♀s.

Matings between F_1 hens out of (BE ♀ × PE ♂) × F_1 ♂s out of BE ♀ × PE ♂ gave

1 BE ♀, 2 BE ♂s, 1 PE ♀.

F_1 hens of this origin were not mated with F_1 ♂s out of PE ♀ × BE ♂.

F_1 hens out of PE ♀ × BE ♂ × F_1 ♂s out of BE ♀ × PE ♂ gave

3 BE ♀s, 6 BE ♂s, 3 PE ♀s.

F_1 hens out of PE ♀ × BE ♂ × F_1 ♂s out of PE ♀ × BE ♂. Only one mating was made which gave 4 BE ♀s. Thus the total numbers from F_1 matings are:

8 BE ♀s, 8 BE ♂s, 4 PE ♀s.

A certain number of matings were also made from F_2 birds, but the analysis of the results obtained is complicated by the fact that the F_2 birds are of different kinds and of various origins, and, therefore, it is impossible to tabulate them separately.

Pooling the results together got from these matings there are:

BE ♀s	BE ♂s	PE ♀s	PE ♂
47	69	53	1

The cases in which the PE cocks appeared will now be dealt with.

BE ♀	♂	BE ♀	BE ♂	PE ♀	PE ♂
73 (bought)	× 23 out of BE × PE	—	—	—	1
202 („)	× 165 „ BE × PE	—	—	2	1
432 (bred by me)	× 342 „ PE × BE	—	3	3	1
		—	3	5	3

Hen 73 was mated with three other cocks:

♀ BE ♂	BE ♀	BE ♂	PE ♀	PE ♂
73 × 102 (out of PE × BE)	—	1	1	—
× 92 („ PE × BE)	—	1	2	—
× 89 („ BE × PE)	1	1	—	—
	1	3	3	—

Her total, therefore, was 1 BE ♀, 3 BE ♂s, 3 PE ♀s, 1 PE ♂.

Hen 202 was mated with two other cocks:

♀ ♂	BE ♀	BE ♂	PE ♀	PE ♂
202 × 172 (out of PE ♀ × BE F_1 ♂)	—	2	1	—
× 216 („ BE ♀ × BE F_1 ♂) (BE × PE)	—	2	—	—
	—	4	1	—

Her total, therefore, was 4 BE ♂s, 3 PE ♀s, 1 PE ♂.

Hen 432 was bred by me. Her mother was a cinnamon hen which was bought, but her father was ♂ 172. ♂ 172 has already appeared in many of the tables showing the origin of BE hens from the mating of BE ♀ × PE ♂. Hen 432 is unfortunately the only bird of the 3 hens used which has any connection with the previously recorded experiments. She was mated with one other cock, No. 513, by whom she had 4 BE ♀s, 3 BE ♂s, 5 PE ♀s. Her total is, therefore, 4 BE ♀s, 6 BE ♂s, 8 PE ♀s, 1 PE ♂. The cocks used in these matings were Nos. 23, 165 and 342. No. 23 was not used again with a BE hen. 165 was used in three other matings and gave:

3 BE ♀s, 2 BE ♂s, 2 PE ♀s,

giving a total of 3 BE ♀s, 3 BE ♂s and 3 PE ♀s. 342 was not used again with a BE hen.

Finally there are the matings between PE hens and F_1 cocks to be considered. These matings should theoretically give equality in eye colours and equality in sex.

Pooling all the results together, regardless of the origin of the various birds used, we have:

BE ♀s	BE ♂s	PE ♀s	PE ♂s
115	75	113	76

(There were also 6 BE birds and 5 PE birds which could not be sexed.)

These results are striking because there is practically an equal number of BE hens and PE hens, and the BE cocks are also in equality with the PE cocks. As before, the hens are in excess.

If we first consider the PE hens used in the matings as being all equal, whatever their origin, and take first the matings in which the cocks were all F_1 cocks out of BE hen and PE cock, the results pooled together are:

BE ♀s	BE ♂s	PE ♀s	PE ♂s
48	28	45	28

In the matings in which the F_1 cock was out of PE hen × BE cock there were:

BE ♀s	BE ♂s	PE ♀s	PE ♂s
37	27	44	30

The remaining birds were got by mating PE hens with heterozygous cocks bred in various ways.

The greater number of the hens used in these experiments were F_1 birds from the matings of BE hen and PE cock. The results can, therefore, be further analysed by comparing the results obtained from mating F_1 birds out of BE hen and PE cock, with cocks for the same mating, with the results obtained from mating F_1 hens with F_1 cocks from the mating PE hen and BE cock.

PE hen F_1 (ex BE ♀ × PE ♂) × F_1 ♂ (ex BE ♀ × PE♂):

BE ♀s	BE ♂s	PE ♀s	PE ♂s
26	23	33	24

PE hen F_1 (ex BE ♀ × PE ♂) × F_1 ♂ (ex PE ♀ × BE ♂).

BE ♀s	BE ♂s	PE ♀s	PE ♂s
14	14	17	14

The other matings made, as stated above, were done with birds of various origins and further analysis is therefore impossible.

The numbers are so small that it is impossible to base any conclusion upon them.

Lizard Canaries.

The Lizard canary is peculiar for its distinctive feather pattern and also for the "cap," a well-defined patch of yellow feathers on the head, generally elliptical, but often crescentic in shape with the points directed forward. The characteristic marking appears after the young bird has lost its nest feathers and acquired adult plumage. In subsequent moults

the pattern gradually disappears and the bird is therefore only in its prime during its first year.

Lizard hens mated with PE ♂s show the same phenomena as does the ordinary BE ♀.

Eight Lizard hens mated with 9 PE cocks produced 17 BE ♂s, 1 BE ♀ and 23 PE ♀s. Many of these did not live to maturity. But there is evidence to show that the characteristic cap can be inherited without the lizard marking.

Four birds only lived to acquire adult plumage.

Two cocks, which were otherwise self-greens, had the cap, but no lizard pattern.

One cock which was variegated had the lizard pattern[1] and the dark feathers. The variegation made it impossible to say whether the cap would have been inherited or not.

One PE ♀ showed no lizard marking or cap.

PE ♀ × lizard cock, 15 hens × 8 lizard cocks were mated and gave 18 BE ♂s and 18 BE ♀s, and 1 not identified. Of these birds 3 ♂s variegated showed lizard markings, 2 ♀s no lizard markings, 3 self-green ♂s showed no lizard marks or cap, 1 ♀ showed cap and no lizard markings, 1 ♀ showed lizard marks, 1 self-green showed cap and no lizard markings.

F_2. BE ♂s and BE ♀s ex mating between PE birds × lizards.

3 BE ♀s × 6 BE ♂s.

9 BE ♂s, 14 BE ♀s, 3 PE ♀s.

Two ♂s had lizard markings, 3 had none. 6 ♀s had lizard markings, 2 had none. PE ♀s, none had lizard markings.

PE ♀s (ex lizard × PE) × BE ♂s (lizard × PE).

2 ♀s × 4 ♂s gave

4 BE ♂s, 7 BE ♀s, 1 PE ♂, 2 PE ♀s, 1 not identified.

Of the BE ♂s only 1 showed lizard markings. Of the BE ♀s 4 had lizard markings and 3 had none. PE birds did not live long enough.

Chrysomitris cucullata *hybrids*.

Chrysomitris cucullata ♂ mated with cinnamon ♀ No. 375 gave 2 young, both cocks, orange-coloured hybrids, Nos. 494 and 495. Mated with cinnamon ♀ 436 he gave 3 young. Two of these were orange and *one was green* and they were all males, Nos. 502, 503, 504. The orange F_1 birds were all alike, and their appearance is accurately given in Plate I, figs. 2 and 3.

[1] This pattern can, in variegated birds, be made out on the dark feathers, though it is of course not traceable on the light feathers.

Cinnamon ♀ × No. 494 F_1 gave PE ♂, BE ♀ and 1 BE, sex not determined. These birds all died in the nest.

Nos. 495 and 502 were infertile or at least failed to breed in their first year, during which only they were tried.

No. 504, orange F_1 ♂, mated with cinnamon ♀ produced 8 young.

2 PE ♂s who did not survive the nest.
1 PE ♀ who did not survive the nest.
2 BE ♂s who did not survive the nest.
2 BE ♂s small, but deep yellow instead of orange.
1 BE ♂ small, with yellow feathers in the tail.

C. cucullata ♀ was mated many times but never produced any eggs.

Unfortunately no drawing of the green hybrid was made, as but for the outbreak of the war would have been done. Its nature is altogether problematical. Conceivably it might be regarded as comparable with "light mules," which can be made from certain canary hens[1], goldfinch ♂s, but the analogy is not very close. It was discovered to be a ♂ on dissection.

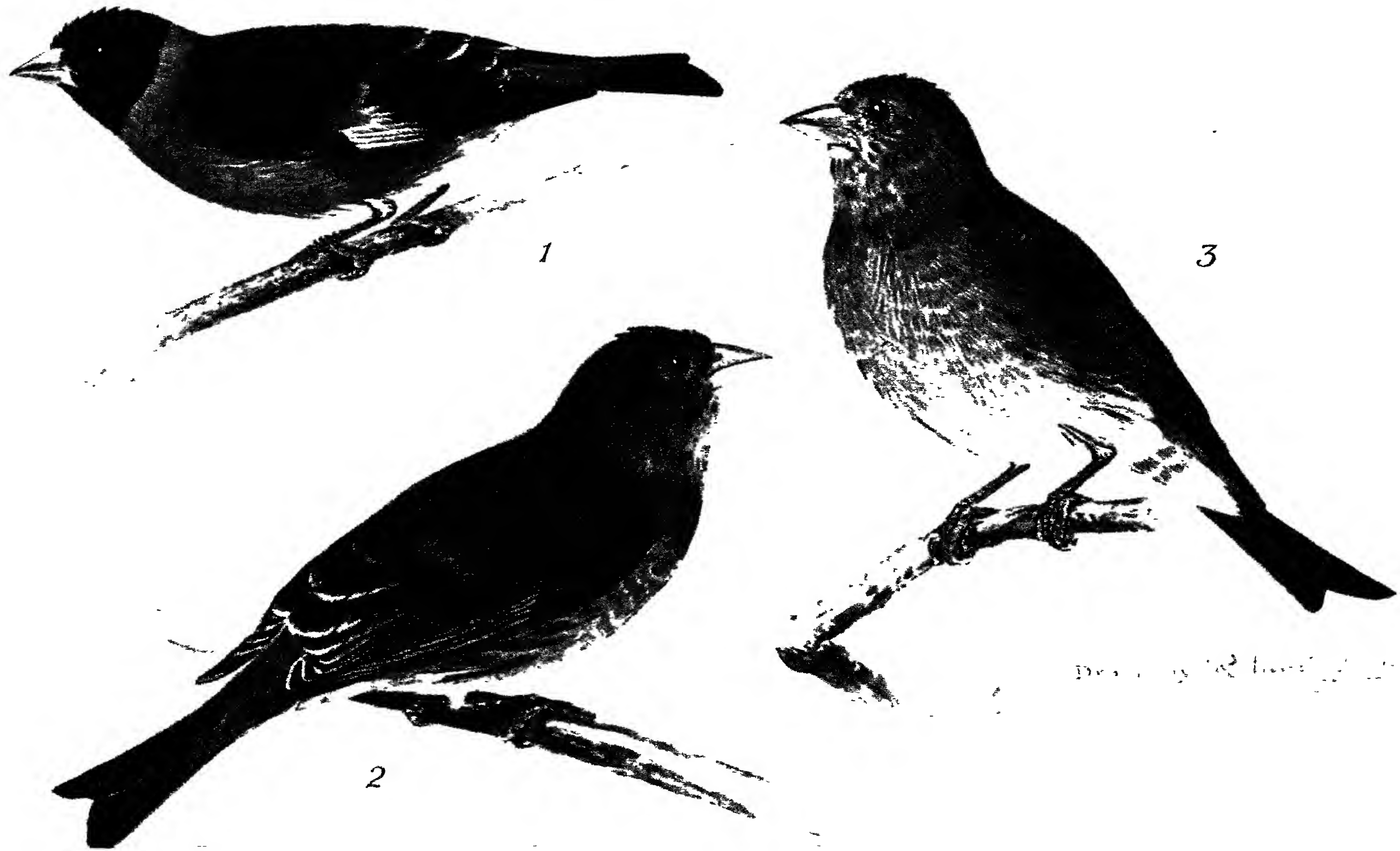
In support of the received account that all the extraordinary modern varieties have been produced from the "wild canary" (*Serinus canarius*), very little positive evidence exists. I had made a search of the literature and was preparing a paper to suggest that the modern forms of canary might have arisen from some such mating as *Chrysomitris citrinella* and canary.

These notes are published in accordance with the wish of Mr Bateson, one of whose last acts was to help me to prepare them for the press. Without his help and encouragement the work would have been impossible. I wish to place on record my gratitude to him.

EXPLANATION OF PLATE I.

Fig. 1. *Chrysomitris cucullata* ♂.
Figs. 2 and 3. F_1 ♂ ♂ ex Cinnamon Canary ♀ × *Chrysomitris cucullata* ♂.

[1] I imported wild canaries from Madeira and from the Canary Islands and attempted to cross them with domestic varieties, but though I tried them both in ordinary cages and in the flight I had no success. Others, I believe, have succeeded. The Mediterranean form is also said to breed with domestic canaries but I never had any of that form.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THE BEHAVIOUR OF POLLEN STARCH IN A GERANIUM AND ITS BUD SPORT.

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(*University of Nebraska.*)

(With Three Text-figures.)

The following paper traces the course of starch disappearance in the pollen of a Geranium and its bud sport. Such information is of interest because of the use which geneticists are making of carbohydrate conditions in pollen as indices of the genetic composition of plants (1, 2, 3). The paper also reports a difference in residual percentages of completely starchy pollen as between this Geranium and its bud sport.

The plants whose pollens we have studied were turned over to the senior writer by Mr Bateson in 1922 for physiological and genetic investigation. They originated in Chard, Somerset, and were described by Bateson (4) in 1921. The type plant, known as Salmon Fringed, is a Pelargonium with salmon coloured, notched petals, defective pistils, and shiny, crinkled, brittle leaves. It produces, quite freely, bud sports of the normal Zonal Geranium sort, having pink, entire petals, perfect flowers, and soft, matt leaves.

Several angles of approach have been tried with indifferent success in revealing information as to the nature and cause of this sporting. The present paper deals with one of those angles, not very fruitful in its direct bearing on the problem in hand perhaps, but suggestive in reference to other lines of genetic work.

The senior writer in 1922 saw some of Renner's (5) *Oenothera* pollens, showing carbohydrate segregation in F_1 hybrids and, at Bateson's suggestion, examined the pollens of the latter's interesting collection of Pelargoniums. It was easy to observe heterogeneity in carbohydrate conditions. Uniformity was the exception rather than the rule—of course the reasonable thing to expect in this highly hybridised genus.

It accordingly became more or less a matter of course to pursue this type of observation in some detail when later investigating the actual genetic composition of the Salmon Fringed Geranium and its Zonal bud sport. If the sporting really involved a shift in genetic character there seemed to be a possibility that a change in ratios of male gametophyte types might also go on.

In both forms the pollen from opened flowers, when tested with iodine, showed a mixture of starchy and non-starchy pollen. But when we counted, our ratios told us nothing except that the condition seemed very capricious. The next step, logically, was to study the starch distribution in flower buds of various degrees of development. We at once found, as did Molisch (6), Lidforss (7), and Tischler (8) for pollens which they studied, that our pollens both passed through a period of starch engorgement some time before anthesis, the starch later disappearing to some extent.

At this time the paper by Nesta Ferguson (9) came to our attention, in which she announced the percentage of sterile pollen in certain plants as a function of the age of the flower. This report made quite clear the necessity for quantitative analysis of the carbohydrate changes in our material, which, like sterility in her examples, was so clearly a progressive affair. We were further encouraged by the hope that such an analysis would reveal a point of relative stability or equilibrium at which we could detect the presence of more than one valid type of male gametophyte and so obtain reliable ratios.

We spent some time working over technique, finding in the end a simple enough way to proceed. The anthers of a given flower may be used indifferently, being well synchronised, but of course the smaller have fewer grains of pollen. Each anther must be stripped clean of its pollen with fine needles in a tiny drop of the fixing solution and then removed from the drop. Chloral hydrate iodine gives vivid slides but they do not last well. They may be kept from crystallising by ringing with hot paraffin or melted vaseline, but they bleach in a few days, and of course swell greatly. Better results are to be had by using a drop of light yellow tincture of iodine which is allowed to dry. This fixes the pollen to the slide, staining the starch and keeping it unchanged (for at least two weeks and doubtless longer) until ready to clear and mount. In mounting, one floods the slide with absolute alcohol, followed either by clove oil or by xylol and balsam. Counting should be done shortly after, for the iodide of starch gradually disappears, being quite gone in slides three months old.

We found that counting was done most quickly and with least error or fatigue by using the Euscope. This is a camera in which the image is projected from the microscope on to a vertical screen. A binocular microscope does nearly as well.

For most of the work plants growing at a greenhouse temperature of 20 to 25 degrees centigrade were used. Later material was run, through

the courtesy of Dr Peltier, of the Nebraska Agricultural Experiment Station, at constant temperatures of 15, 20, 25 and 30 degrees centigrade. Bud lengths were measured to the nearest millimetre and slides prepared in duplicate. A typical mount would be counted in from three to six fields, each showing from fifteen to fifty or more grains.

The data are summarised in the tables which follow and in graphs, Figs. 1–3.

TABLE I.

Pollen grains of Pelargonium, Salmon Fringed, classified according to starch content at successive stages of growth. Greenhouse temperature, 20–25° C.

Bud length mm.	Starch content: Full	Part	None	Total pollen	Proportion in total of full
6	114	13	0	127	·90
	129	18	0	147	·87
7	113	11	0	124	·91
	160	22	0	182	·87
	195	7	0	202	·97
	186	14	0	200	·93
8	197	10	0	207	·95
	243	24	1	268	·90
	283	1	2	286	·99
	241	0	4	245	·98
9	246	24	2	272	·90
	172	16	0	188	·91
	92	2	1	95	·97
	379	7	8	394	·96
10	151	16	0	167	·90
	161	18	0	179	·90
	157	3	1	161	·97
	227	6	3	236	·96
11	197	22	0	219	·90
	162	31	0	193	·83
	279	1	0	280	·99
	324	1	1	326	·99
12	235	24	0	259	·91
	192	26	0	218	·89
	272	3	1	276	·99
	605	2	5	612	·90
13	87	35	0	122	·71
	131	73	6	210	·63
14	35	69	7	111	·31
	31	59	2	92	·33
15	16	107	3	126	·14
	11	83	0	94	·11
	14	63	0	77	·18
16	3	35	0	38	·08
18	7	104	1	112	·06
	10	80	0	90	·11
20	6	76	2	84	·14
	6	123	0	129	·05
	7	115	5	127	·05
	4	175	4	183	·02

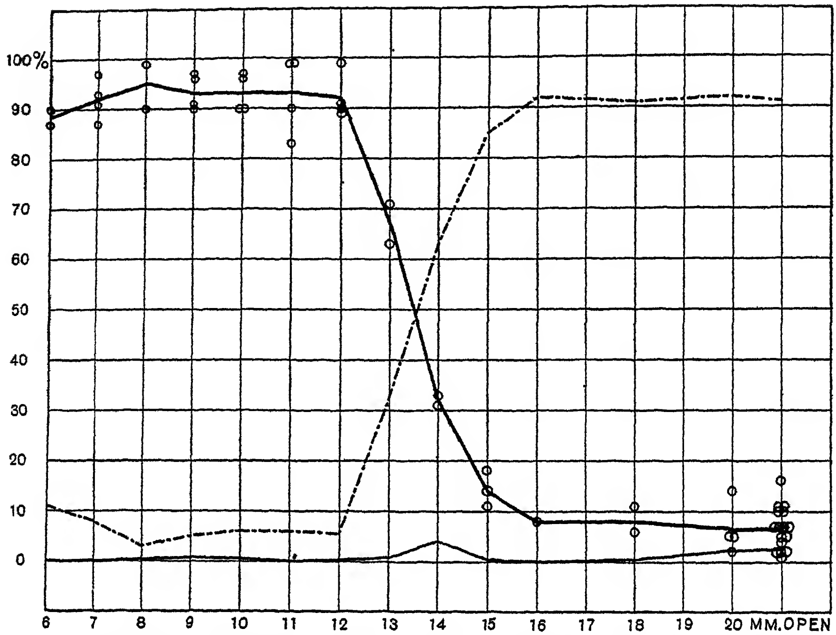

Fig. 1. Carbohydrate changes in pollen, Salmon Fringed Geranium. Heavy line, mean percentages starch-filled pollen; light line, mean percentages starch-free; broken line, mean percentages partly starchy. Ordinates percentages, abscissae bud lengths in mm.

TABLE I A.

Pollen grains of open flowers of Pelargonium, Salmon Fringed, classified according to starch content. Greenhouse temperature, 20–25° C.

	Starch content				
	Full	Part	None	Total pollen	Proportion in total of full
	7	63	0	70	·10
	3	135	5	143	·02
	5	56	14	75	·07
	7	87	3	97	·07
	4	90	0	94	·04
	10	51	1	62	·16
	8	63	0	71	·11
	4	80	2	86	·05
	1	56	0	57	·02
	13	101	2	116	·11
	7	119	2	128	·05
	13	110	1	124	·10
	7	86	1	94	·07
	3	169	6	178	·02
	4	50	1	55	·07
	7	109	0	116	·06
	1	69	1	71	·01
Total	104	1494	39	1637	
Mean proportion full ...	...	...	...	... ...	·066
Proportion full, from totals ...	...	...	...	... ...	·064–

In Table I are summarised the actual counts of pollen grains in various conditions of starch content at bud lengths from 6 mm. up to anthesis, for Salmon Fringed. This table, like the three which follow it, combines the experiments run at a greenhouse temperature of 20–25° C. with those run at a constant temperature of 20°. That this has not prevented a fairly close grouping of cases along the mean is shown by the circles and heavy line in Fig. 1.

This table makes clear the necessity for a distinction between pollen grains having some starch and those which are full of starch. The reciprocal relation between fully starchy and partly starchy pollen is well shown in Fig. 1.

This graph also illustrates the existence of two periods of relative stability. In buds from 8 to 12 mm. close to 93 per cent. of pollen is completely starch filled, about 5 per cent. is partly so, and a fluctuating remainder has no starch. Between 12 and 15 mm. there is a rapid digestion of starch (to reducing substance, Flückiger's test), but no corresponding increase in the number of starch-free grains. From 16 mm. on to anthesis is another period of relative stability. At opening the Salmon Fringed shows (Table I A) over 6 per cent. of pollen still completely starchy. Many, but not all, of these grains are smaller than normal and thicker walled. Between 2 and 3 per cent. of the grains are quite starch-free, while about 91 per cent. are partly starchy.

The same general type of behaviour is found to hold for the Zonal bud sport, Tables II and II A, and Fig. 2. Here again we have two periods of relative equilibrium. During the first period about 93 per cent. of pollen is completely starchy, and nearly 7 per cent. partly so, a fluctuating amount, less than 1 per cent., being starch-free. The second equilibrium seems to be characterised by over 3 per cent. completely starchy, over 4 per cent. starch-free, and about 92 per cent. partly starchy.

The two curves of mean percentages, completely starchy pollen, are superposed in Fig. 3. While very similar in general, the interesting differences in rates of change above detailed are evident. At anthesis the Salmon Fringed Geranium contains almost exactly twice the percentage of starch-filled pollen shown by its bud sport, the Zonal (cf. Tables I A and II A). The question may fairly be raised whether this difference is due to a segregation of actual pollen types, or to a difference in physiological capacities of the two plants. In any case it seems reasonable to suppose that it has a genetic basis. Like the case recently reported by Huxley and Ford (10) it is a difference finding expression in the rate of a physiological process.

TABLE II.

Pollen grains of Pelargonium, Zonal bud sport, classified according to starch content at successive stages of growth. Greenhouse temperature, 20–25° C.

Bud length mm.	Starch content Full	Part	None	Total pollen	Proportion in total of full
7	168	14	0	182	·92
	177	10	0	187	·94
8	120	8	0	128	·94
	151	10	0	161	·93
	46	2	1	49	·98
9	299	8	0	307	·96
	210	9	0	219	·95
	207	114	1	322	·64*
10	183	14	0	197	·92
	286	29	0	315	·90
	210	0	3	213	·98
	308	0	1	309	1·00−
11	143	19	0	162	·88
	128	24	0	152	·84
12	134	17	0	151	·88
	149	11	0	160	·92
	168	2	1	171	·98
	246	5	5	256	·96
13	164	107	0	271	·60
	112	51	3	166	·67
14	33	138	0	171	·19
15	17	100	2	119	·14
	20	119	1	140	·14
16	13	110	1	124	·10
	23	102	0	125	·18
17	30	235	0	265	·11
	20	176	0	196	·10
18	26	242	0	268	·10
	10	139	6	155	·06
20	12	211	9	232	·05
	4	157	3	164	·02
	7	208	12	227	·03

* Probably defective strain; 5 out of 6 fields counted showed over ·90.

TABLE II A.

Pollen grains of open flowers of Pelargonium, Zonal bud sport, classified according to starch content. Greenhouse temperature, 20–25° C.

	Starch content Full	Part	None	Total pollen	Proportion in total of full
	10	322	2	334	·03
	17	151	5	173	·09
	10	364	10	384	·03
	11	569	15	595	·02
	3	128	11	142	·02
	3	76	8	87	·03
	0	125	26	151	·00
	0	144	9	153	·00
	3	212	15	230	·01
	4	170	7	181	·02
	8	163	1	172	·05
	5	68	6	79	·06
	15	94	0	109	·14
	10	203	7	220	·04
	3	152	10	165	·02
	13	150	6	169	·08
	1	239	35	275	·00
	9	144	1	154	·06
Total ...	125	3474	174	3773	
Mean percentage full ...	...	...	...	...	·038
Percentage full, from totals	...	...	...	...	·033

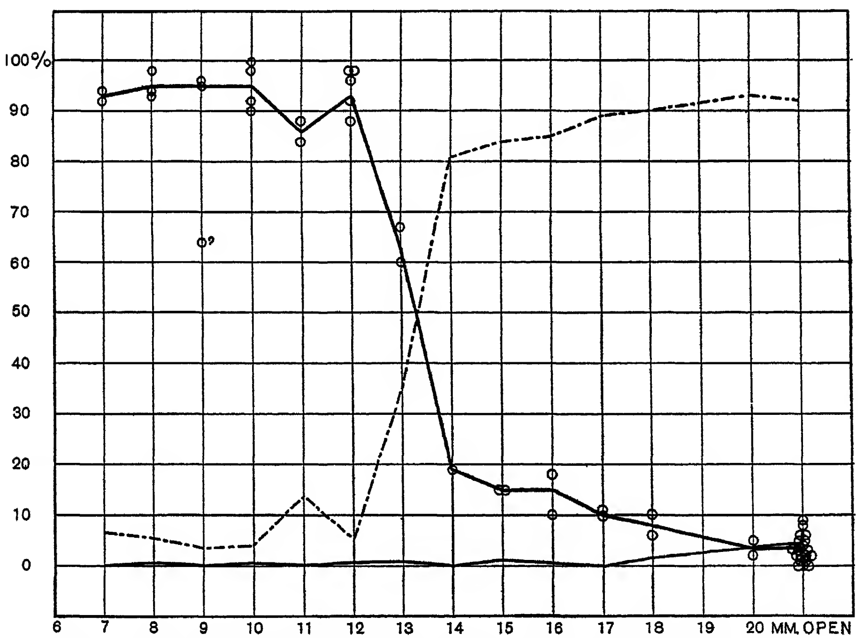

Fig. 2. Carbohydrate changes in pollen, Zonal bud sport. See explanation, Fig. 1.

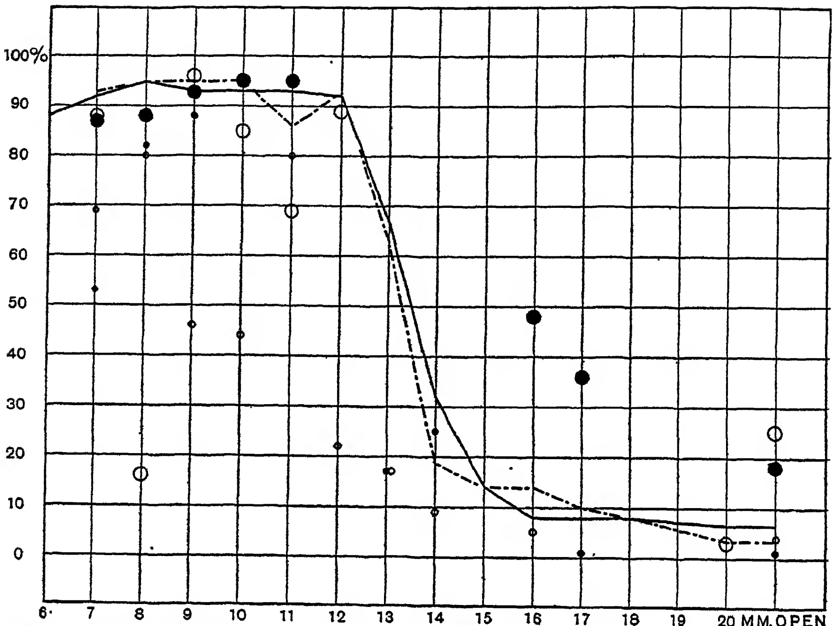

Fig. 3. Temperature effect on pollen starch. Mean percentages starch-filled pollen at greenhouse temperature, 20–25° C., and observations at 15° (large circles) and 30° (small circles). Salmon Fringed shown by solid line and circles, Zonal by others.

TABLE III.

Summary of observed temperature effects on pollen starch of Pelargonium, Salmon Fringed.

Bud length mm.	Mean percentages of starch-filled pollen			
	15°	20–25°	25°	30°
6	—	88	—	—
7	87	92	63	53
8	88	95	93	82
9	93	93	—	88
10	95	93	90	—
11	95	93	—	—
12	—	92	—	—
13	—	67	—	17
14	—	32	—	25
15	—	14	—	—
16	48	8	—	—
17	36	—	—	1
18	—	8	2	—
20	—	6	2	—
Open	18	6	2	1

Fig. 3 also shows some of the more striking temperature data summarised in Tables III and IV. These data illustrate what was repeatedly confirmed by qualitative observation—that high temperature hastens starch disappearance and low temperature delays it. Behaviour is apt to be erratic at both extremes. The necessity for making determinations of the carbohydrate condition at the proper physiological temperature would seem to require no further emphasis than the graphs give.

TABLE IV.

Summary of observed temperature effects on pollen starch of Pelargonium, Zonal bud sport.

Bud length mm.	Mean percentage of starch-filled pollen 15°	20–25°	25°	30°
7	88	93	92	69
8	16	95	79	80
9	96	95	95	46
10	85	95	90	44
11	69	86	57	80
12	89	93	75	22
13	—	63	4	17
14	—	19	53	9
15	—	14	49	—
16	—	14	—	5
17	—	10	—	—
18	—	8	2	—
20	3	3	1	—
Open	25	3	2	4

Incidentally these temperature experiments with those of Renner (*loc. cit.*) on ripe pollen may aid in clarifying the observations of Lidforss (7). The latter noted that the period of maximum starch content persisted through anthesis in northern European anemophilous pollens but not in southern ones. His explanation was that the northern were under greater necessity of conserving their carbohydrates because of poorer photosynthetic conditions. The observations of Tischler (*loc. cit.*) on numerous tropical pollens are also interesting in this connection.

It must be borne in mind that the carbohydrate changes we have traced do not bring about a static condition in the pollen, but are themselves subject to later modification by respiration, autolysis and bacterial action. Such changes, familiar in herbarium material and pollen collections, must ultimately destroy all pollen starch not utilised in growth, thus obscuring any genetic distinctions based on starch content. What we have called a second equilibrium is of course transient, but not necessarily on that account either imaginary or indefinite.

In conclusion, it seems reasonable that whether size, shape, or colour

reaction of pollen carbohydrate grains be used in genetic analysis the march of carbohydrate change ought to be understood beforehand, and such factors as temperature ought to be considered. Further, it is likely that if the above precautions are taken there may be numerous cases in which digestion rates themselves may supply useful criteria of genetic conditions.

Summary.

The pollen of the Pelargonium, Salmon Fringed, and its Zonal bud sport can be classified into starch-filled, partly starchy, and starch-free.

In both cases the percentage of starch-filled reaches a maximum of about 93 per cent. in buds of 8 to 12 mm. length, then drops rapidly to about 15 per cent. in buds 15 mm. long. From this point on to anthesis the change is slower, reaching an equilibrium at about 20 mm.

The pollen of open flowers of Salmon Fringed has almost exactly twice (6·4–6·6 per cent.) the percentage of starch-filled pollen shown by its bud sport (3·3–3·8 per cent.). This is an expression of a difference in rate of starch digestion.

Temperatures of 25 and 30° C. hasten starch digestion, while 15° retards it. Behaviour at both extremes is erratic.

Analysis of pollen carbohydrate conditions for genetical purposes can perhaps be facilitated by the foregoing physiological considerations.

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CHROMOSOME BEHAVIOUR IN TRIPLOID WHEAT HYBRIDS.

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(With Eight Text-figures.)

According to Sax (3) the behaviour of the chromosomes during the reduction divisions in the triploid hybrid between *Triticum monococcum* and *T. turgidum* is very different from that in all pentaploid wheat hybrids which have been studied. In both cases 7 univalent chromosomes appear but whereas in the pentaploids these all divide equationally at the heterotypic division and wander undivided to the poles at the homeotypic, in the triploid hybrid the reverse is true, the equational splitting failing at the first and occurring at the second division. Kihara (1) on the other hand finds in the triploid hybrid between *T. monococcum* and *T. dicoccum* a behaviour resembling that in pentaploids except that the number of bivalents is variable, and that some of the univalents fail to divide at the heterotypic division.

I have recently examined abundant material of a hybrid between *T. monococcum* (einkorn) and a variety of *T. turgidum* which I received from the Division of Botany of the Dominion Department of Agriculture. Dr Güssow, head of the Division, states that this variety came from Tunis and is known to him only under the Arabic name. According to Percival's (2) classification it is *T. turgidum* var. *buccale*. It crosses readily with "einkorn," and the hybrids are very vigorous and not quite completely sterile, averaging about 4 seeds per plant. The material was examined in iron-aceto-carmine, after the stamens had been fixed in Carnoy's solution and transferred gradually to 70 per cent. alcohol (4). Such preparations of this material are beautifully clear.

The chromosomes of the parental forms used are quite typical for their species, 7 (haploid) in *monococcum*, and 14 in *turgidum*.

At the heterotypic division of the hybrid 3, 4 (Fig. 1), 5, 6 (Fig. 2), or 7 bivalent chromosomes appear. Very rarely does one find 3 and only occasionally 7; the usual number is 5 or 6. The univalent chromosomes number 15, 13, 11, 9 or 7 depending on the number of bivalents. The number of univalents plus twice the number of bivalents is invariably 21. These numbers are different from those reported by Sax (3) for another cross between these two species, for he found 7 bivalents and 7 univalents.

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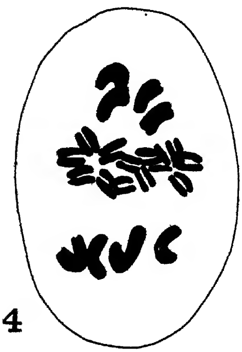

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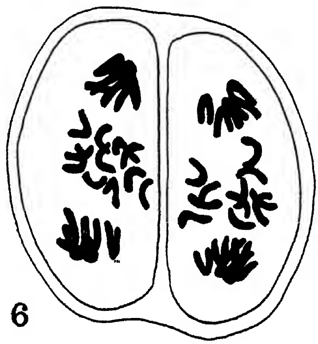

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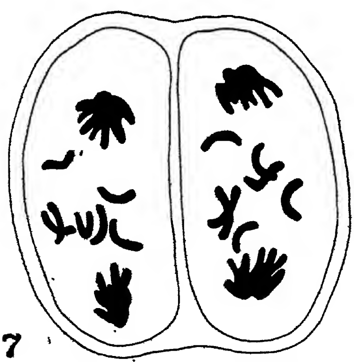

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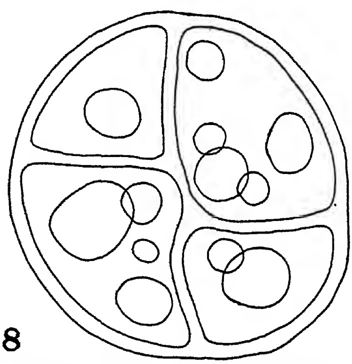

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Fig. 1. F_1 of *T. monococcum* × *T. turgidum*, heterotypic metaphase with 4 bivalent and 13 univalent chromosomes.
Fig. 2. The same with 6 bivalents and 9 univalents.
Fig. 3. Heterotypic anaphase with 9 lagging univalents dividing equationally.
Fig. 4. The same with 13 dividing univalents.
Fig. 5. The same with 9 univalents divided into 2 groups.
Fig. 6. Homeotypic anaphase with 11 lagging undivided univalents.
Fig. 7. The same with 7 univalents.
Fig. 8. Young tetrad with supernumerary nuclei.

All figures were drawn with a 3 mm. apochromatic objective, 25 × eyepiece, and camera lucida and reduced to ½ in reproduction. (Magnification 900.)

They are similar, however, to those found by Kihara(1) in *T. monococcum* × *T. dicoccum*, except that no mother-cells with only 3 bivalents were seen by him.

The association of the two members of a bivalent is usually not so close as in the pure species. They are comparatively long and slender and usually found attached only at one end.

Most of the univalents are usually found at some distance from the metaphase plate of bivalents, though more of them are generally at the edge of the plate than in pentaploid hybrids. In a few cases nearly all of them are in the plate. After the bivalents have divided all the univalents arrange themselves at the equator in strikingly regular fashion (Figs. 3 and 4), and each divides equationally. No matter what the number is, in most cases all move on to the plate and divide. Occasionally one remains at or near the pole without dividing, and occasionally 2 halves appear to be moving to the pole together. But this is rare. The regularity of the behaviour in most cases is evident. It is easy to find dividing mother cells with 4 groups of chromosomes—at each pole a group of divided bivalents, and between them 2 groups of divided univalents (Fig. 5). In the aceto-carmine material the univalents may be counted with ease in side views. They move to the poles in a fairly regular row and all usually become incorporated in the daughter-nucleus. There is very little chromosome loss at this division.

In Sax's material the procedure is quite different. None of the univalents move into the equatorial position. All remain undivided at or near the poles in the position which they occupied when the bivalents were in metaphase. The number at either pole is a matter of chance so that each daughter-cell receives 7 halves of bivalents and 0–7 (usually 3 or 4) univalents. In my material each receives 3 to 7 halves of bivalents and 15 to 7 halves of univalents. In Kihara's material of *T. monococcum* × *T. dicoccum* some of the univalents always divide and some usually fail to divide. The number of lagging univalents is usually less than 7, showing that a number must have failed to move into the equatorial position, since usually more than 7 are seen at metaphase of bivalents.

At the homeotypic division a regular plate which includes all the chromosomes is formed. A number of these (the bivalents) divide while the rest (the univalents) remain undivided near the centre (Figs. 6 and 7), and then move slowly after the others towards one pole or the other at random. The number of these lagging, undivided chromosomes varies through about the same range as that of the univalents at the heterotypic

division. The higher numbers are not quite so frequent and occasionally fewer than 7 are seen, showing that an occasional univalent may fail to divide at the heterotypic division.

Sax found the behaviour difficult to determine at the homeotypic division in his material but is of the opinion that all chromosomes divide. This would be expected since they are all either divided bivalents or undivided univalents. Kihara reports that the usual numbers of lagging undivided chromosomes in *T. monococcum* × *T. turgidum* are 1 to 4. Evidently a considerable proportion of univalents divide at this division, having failed to do so at the first.

Owing to the tardiness of the univalent chromosomes in moving at random to the poles, several usually fail to become incorporated in the new nucleus. These form one or more small nuclei. The young tetrads therefore present a very abnormal appearance. In addition to a main nucleus each cell usually contains several small nuclei (Fig. 8). Rarely, however, do these small nuclei become enclosed in cells of their own, so that almost always only 4 pollen grains result from each mother-cell. Sax finds normal tetrads and Kihara frequent supernumerary nuclei.

Only about 2 per cent. of the mature pollen grains show stainable cytoplasm. Even in these the cytoplasm is often shrivelled. As might be expected, therefore, the plants are nearly sterile. Six hybrid plants have been grown and though all were very vigorous, they produced only about 4 grains per plant. In this case the sterility is evidently gametic and not zygotic as Kihara maintains for pentaploid hybrids.

It is evident from this account that the behaviour in my material is similar to that in pentaploid wheat hybrids. The chief difference is in the variable number of bivalents. In pentaploids all bivalents possible (14) from 5 sets of 7 single chromosomes are formed. In this triploid hybrid all possible bivalents (7) from 3 sets of 7 are occasionally formed. But commonly 1 or 2, sometimes 3, and rarely 4 pairs fail to mate. The number of univalents is of course correspondingly increased. It appears that since the original duplication which produced *T. turgidum* and its relatives, some of the chromosomes have become so modified that they have difficulty in mating with those of the original form in which no duplication occurred. Differentiation has not gone so far as entirely to prevent mating but it has made mating difficult. Even in the case of those pairs which always mate, the association is not so intimate as in the pure species.

It is conceivable that the bivalents are formed from the 2 sets of *turgidum* chromosomes, leaving the *monococcum* ones as univalents. But

this is not likely to be the case since each *turgidum* chromosome finds a mate among *vulgare* chromosomes and *vulgare* ones are unable to mate among themselves when they have an opportunity to do so in wheat-rye hybrids (5). In the latter no bivalents are usually formed, the number of chromosomes appearing at the heterotypic division being the sum of the haploid numbers of the parents.

In the variable amount of mating this triploid hybrid between *T. monococcum* and *T. turgidum* resembles that between the former and *T. dicoccum*. In most other points of behaviour the resemblance is also close. An exception is in regard to the failure of some of the univalents in the *dicoccum* hybrid to divide at the heterotypic division.

In view of these resemblances it is surprising to find the behaviour so different in the hybrid between *T. monococcum* and another variety of *T. turgidum*, as reported by Sax. The variety which I used behaves normally in crosses with all other 14 chromosome species, including *T. dicoccum*, and all chromosomes in these hybrids mate. The variety used by Sax was Alaska, which belongs to that section of the species which has the conspicuously branched ears. It is possible that this character is more important than indicated in taxonomic works. At any rate it appears that there are marked chromosome differences within *T. turgidum*.

Summary.

At the heterotypic division of the hybrid between *T. monococcum* and a variety of *T. turgidum* 3 to 7 bivalent and 15, 13, 11, 9 or 7 univalent chromosomes appear. After the bivalents have divided the univalents all arrange themselves on the plate and divide equationally. At the homeotypic division some chromosomes lag, fail to divide, and wander at random to the poles. Their number corresponds to that of the univalents of the first division.

This behaviour is similar to that in pentaploid hybrids except in regard to the variable amount of mating. It is very different from that in another cross between these same two species, investigated by Sax, in which 7 bivalents and 7 univalents appear and in which the univalents divide at the second division instead of the first. Nevertheless it is similar to that in *T. monococcum* × *T. dicoccum*, except that in the latter a number of univalents fail to divide at the heterotypic division.

Since the original duplication which produced 14 chromosome species, such differentiation has occurred as to make mating between chromosomes of the two types difficult.

Chromosomes of two varieties of *T. turgidum* appear to be differentiated as judged by their behaviour in hybrids, though those of one behave normally in crosses with entirely different species of wheat.

This investigation is part of a study being carried on with the aid of a grant from the National Research Council.

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THE MORPHOLOGY AND CYTOLOGY OF SOME HYBRIDS OF *AEGILOPS OVATA* L. ♀ × WHEATS ♂.

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(With Five Plates.)

The occurrence of natural hybrids of *Aegilops ovata* with Bread Wheat (*Triticum vulgare* Host.) has been frequently observed and recorded since the discovery of *A. ovata* × *T. vulgare* by Requien, round Avignon and Nîmes (S. France), in 1821–4.

Not suspecting its origin, Requien named the plant *Aegilops triticoides*, and it was not until the investigations and experiments of Fabre, Godron (4), Regel, Groenland (5) and Planchon, about forty years later, that its hybrid origin was established.

Natural hybrids occur wherever *A. ovata* is found growing in or near wheat fields, and two examples have appeared among sowings of this plant in my experimental cages at Reading.

When dug up and carefully examined these hybrids are generally seen to spring from a buried ear or spikelet of *Aegilops*, the *Aegilops* being almost invariably the mother plant.

Hybrids, chiefly of *A. ovata* ♀ × *T. vulgare* ♂, produced by carefully controlled crossing have been obtained by Planchon, Godron (4), Vilmorin, Groenland, Tschermak, Bally (2) and others, but none of these have given detailed accounts either of the parents or the hybrids.

During the last four years I have succeeded in obtaining the following hybrids:

A. ovata ♀ × *T. dicoccoides* ♂ (Wild Emmer).
var. *Kotschyanum*.
var. *spontaneonigrum*.
× *T. dicoccum* var. *Ajar* ♂ (Abyssinian Emmer).
× *T. durum* ♂ (Macaroni Wheat).
var. *affine*.
× *T. vulgare* ♂ (Bread Wheat).
var. *erythrospermum* (Greek form).
var. *albidum* (Starling).
var. *milturum* (Solino d'Ascoli, Spain).

Descriptions of these and their parents grown under similar conditions are presented below, together with observations upon their

morphological and cytological characters, and the appearance of the parental characters in the hybrids.

When sown in autumn *A. ovata* comes into ear and flowers earlier than wheats sown at the same time. In order to obtain both in a suitable state of development for hybridisation, short rows of the *Aegilops* were sown at fortnightly intervals from September to March; plants of the January and February sowings flowered about the same time as wheats sown in October.

Crossing was carried out on *Aegilops* plants grown in the greenhouse and in the open ground, and in both cases I had few failures; a few reciprocal crosses with wheat as the mother parent gave negative results.

Aegilops ovata L. (*A*, Plate II).

Culm: 45–55 cm. high; middle of the upper internode 1–1·25 mm. in diameter, hollow, with thin walls.

Inflorescence: 3–3·6 cm. long, the whole disarticulating at the first node of the rachis, a small abortive spikelet remaining attached to the culm. The rachis is very tough, its surface clothed with short scabrid hairs; each internode 5–10 mm. long, thin and wedge-shaped, from 2–3 mm. wide at the apex, 1 mm. across the base.

Spikelets: 3–5, 1·5 cm. long apart from the awns, one or two lowest rudimentary, the upper spikelets usually 4-flowered, the two upper flowers of these spikelets sterile; rachilla hairy all over.

Empty glume: pale straw colour, 10 mm. long, 7–8 mm. broad, rigid, rounded on the back without a keel, but with 9–10 prominent scabrid ribs; margins hairy; awns scabrid, 4–5, one of them often very short, the rest 2·5–4 cm. long in the upper spikelets, 1·5–2·2 cm. in the lower; the glumes overlap slightly and completely surround the rest of the spikelet.

Flowering glume: 10 mm. long, awned, 5–6-nerved, the outer surface of the upper part hairy, the lower half glabrous; margins slightly hairy; awns 2 and a short tooth, one awn usually 2–3 cm. long, the other 1–2 cm. long.

Palea: thin, awnless, bicarinate, keels hairy, surfaces with short hairs. On the upper surface of the leaf blades, auricles and margins of the lower leaf sheaths are a few long hairs.

Wild Emmer, *Triticum dicoccoides* Körn. var. *Kotschyanum* Perciv. (*B*, Plate II).

Culm: 120 cm. long; middle of the upper internode 2 mm. in diameter, solid.

Inflorescence: 8–9 mm. long; rachis very fragile, disarticulating easily at each node when ripe; each internode 3–4 mm. long, wedge-shaped, 2 mm. across the apex, 1 mm. across the base; margins fringed with long hairs, some 2–3 mm. long; frontal tuft conspicuous, its hairs up to 5 mm. long.

Spikelets: 16–18, each 15–17 mm. long, 3-flowered, 2 flowers fertile; rachilla with very short hairs.

Empty glume: white or pale red, glabrous, tough, 10–12 mm. long, 4 mm. across the face; keel prominent from the apex to the base; keel tooth 1 mm. long, acute; lateral nerve prominent, ending in a short tooth.

Flowering glume: glabrous, 13–14 mm. long, 9–10 nerved; awn scabrid, 10–14 cm. long.

Leaf blades: clothed with short hairs; long hairs on the auricles.

Hybrid, *A. ovata* ♀ × *T. dicoccoides* var. *Kotschyanum* ♂ (*A* × *B*, Plate II).

Culm: 45–55 cm. long; middle of the upper internode 1·5 mm. in diameter; nearly solid.

Inflorescence: 7–8 cm. long; rachis very fragile, disarticulating very easily at the nodes as in the Emmer parent; each internode 6–8 mm. long, wedge-shaped, 4 mm. across the apex, 3 mm. across the base; margins hairy; frontal tuft short.

Spikelets: 7–9, 4-flowered, sterile; rachilla hairy.

Empty glume: white, scabrid, tough, 11–12 mm. long, 5 mm. across the face, with 8–10 prominent ribs including the keel; awns 2 with a tooth or short point between them, the keel awn 3–5 cm. long, the lateral awn 1·5–1·8 cm. long.

Flowering glume: 11–12 mm. long, glabrous, 7–8-nerved; awn on the lower spikelets 5–6 cm. long, on the upper spikelets 7·5 cm. long.

Leaves: a pale green colour, their upper surfaces with scabrid points; a few long hairs on the auricles; no long hairs on the leaf blades.

Wild Emmer, *Triticum dicoccoides* Körn. var. *spontaneonigrum* Perciv. (*C*, Plate II).

Culm: 110 cm. long; middle of the upper internode 2 mm. in diameter, solid.

Inflorescence: 8·5–9·5 cm. long; rachis fragile, separating easily at the nodes when ripe; each internode 4–5 mm. long, wedge-shaped, 2 mm. across the apex, 1 mm. across the base; margins fringed with long hairs, some 1–2 mm. long; frontal tuft long.

Spikelets: 16–18, each 15 mm. long, 6 mm. broad; 3-flowered, 2 flowers fertile; rachilla glabrous.

Empty glume: lower half black, the upper half white or pale red, 12 mm. long, 3 mm. across the face; keel and one lateral rib prominent and scabrid; keel tooth short, blunt; empty glumes separated.

Flowering glume: 13–15 mm. long, 10–12-nerved, glabrous, exposed part black, the covered portion pale yellow; awn scabrid, 10–13 cm. long.

Leaf blades: pale green, with short soft hairs on their surfaces.

Hybrid, *A. ovata* ♀ × *T. dicoccoides* var. *spontaneonigrum* ♂ (*A* × *C*, Plate II).

Culm: 60 cm. long; middle of the upper internode 1·5 mm. in diameter, hollow with thick walls.

Inflorescence: 8 cm. long; rachis somewhat fragile but disarticulating at the nodes less easily than the Emmer parent, especially in the upper part of the ear; each internode 6–8 mm. long wedge-shaped, 4 mm. across the apex, 2 mm. across the base; margins fringed with hairs shorter than those of the Emmer parent; frontal tuft small.

Spikelets: 10–11, each 15 mm. long, 4-flowered, 2 flowers fertile, rachilla hairy.

Empty glume: reddish brown, with black stripes or spots, 12 mm. long; awns 2, with a short tooth between them, keel awn 3–5 cm. long, the lateral awn 2·3–5 cm. long; the margins of the empty glumes overlap slightly.

Flowering glume: glabrous, pale yellow, 12 mm. long, 8–9-nerved; awn 7–9 cm. long, scabrid.

Leaf blades: pale green; hairs on the surfaces resembling those of both parents.

Abyssinian Emmer, *Triticum dicoccum* Schüb. var. *Ajar* Perciv. (*D*, Plate II).

Culm: 65–70 cm. long; middle of the upper internode 2 mm. in diameter, hollow with thick walls.

Inflorescence: 6–7 cm. long; rachis fragile, separating easily at each node; each internode 2 mm. long, wedge-shaped, 1·5 mm. across the apex, 1 mm. across the base; margins fringed with short hairs; frontal tuft small.

Spikelets: 16–19, each 10–13 mm. long, 6–7 mm. broad, 3-flowered, 2 flowers fertile; rachilla glabrous.

Empty glume: white, glabrous, 10 mm. long, 3 mm. across the face; keel and one lateral rib prominent; keel tooth short and blunt.

Flowering glume: 15 mm. long, glabrous, 10-nerved; awn scabrid, 9–12 cm. long.

Hybrid, *A. ovata* ♀ × *T. dicoccum* var. *Ajar* ♂ (*A* × *D*, Plate II).

Culm: 70–75 cm. long; middle of the upper internode 2 mm. in diameter, hollow with thick walls.

Inflorescence: 7·5–8 cm. long, longer than either parent; disarticulating as a whole, as in *A. ovata*; rachis somewhat tough, and does not break so easily at the nodes as the Emmer parent; each internode 7 mm. long, wedge-shaped, 3–4 mm. across the apex, 2 mm. across the base.

Spikelets: 9, each 15 mm. long, 6–7 mm. broad, larger than those of either parent, 4-flowered, sterile.

Empty glume: white, 12 mm. long, 5–6 mm. across the face, with 5–7 scabrid ribs including the keel; keel prominent from apex to base; empty glumes of the lower spikelets with one awn, 2 cm. long, and a short tooth, those of the upper spikelets with 2 awns and a short tooth between them, the keel awn 4 cm. long, the shorter lateral awn 1–1·2 cm. long.

Flowering glume: 10 mm. long, 4–6-nerved, awned, awn of the lower glumes of the spikelet 8–9 cm. long, those of the two upper glumes 5–6 cm. and 1–1·5 cm. long respectively.

Leaf blades and auricles with long hairs; lower leaf sheaths and their margins with shorter hairs.

Macaroni Wheat, *Triticum durum* Desf. var. *affine* Körn. (Sorrentino form) (*E*, Plate II).

Culm: 140–150 cm. long; middle of the upper internode 2–2·5 mm. in diameter, solid.

Inflorescence: 6–7 cm. long; rachis tough; each internode 3–4 mm. long, 2–3 mm. wide; margins fringed with long hairs, some 2 mm. long; frontal tuft well developed.

Spikelets: 18–22, each 10–12 mm. long, 4-flowered, 2–3 flowers fertile; rachilla hairy.

Empty glume: white, glabrous, 9–10 mm. long, 4 mm. across the face; keel prominent from apex to base; keel tooth strong, curved, acute, 1 mm. long, lateral tooth very short or absent; the empty glumes widely separated.

Flowering glume: 10–11 mm. long, glabrous, 12–14-nerved; awn, 12–16 cm. long, the base glabrous or only slightly scabrid.

Leaf blades: glabrous.

Hybrid, *A. ovata* ♀ × *T. durum* var. *affine* ♂ (*A* × *E*, Plate II).

Culm: 70–80 cm. long; middle of the upper internode 2 mm. in diameter, almost solid.

Inflorescence: 7–8 cm. long; disarticulation as in *A. ovata*; rachis tough; each internode 6–7 mm. long, wedge-shaped, 4 mm. across the apex, 2 mm. across the base; margins fringed with short hairs; frontal tuft small.

Spikelets: 10–11, each 15 mm. long, 4-flowered, sterile; rachilla hairy.

Empty glume: white, very tough, 10–12 mm. long, 4 mm. across the face; keel not so prominent as in the wheat parent; awns 2, the keel awns of the lower spikelets 2·8–3 cm. long, of the upper spikelets 6 cm. long; the second awn on each glume of the lower spikelets 1 cm. long, of the upper spikelets 2·5 cm. long; the margins of the empty glumes meet but do not overlap.

Flowering glume: 10–11 mm. long, glabrous, 8–9-nerved; awns 8–9 cm. long, very scabrid.

Leaf blades: glabrous as in the wheat parent; margins of the lower leaf sheaths slightly hairy. The whole plant very glaucous.

Bread Wheat, *Triticum vulgare* Host. var. *erythrospermum* Körn. (a Greek form) (*F*, Plate II).

Culm: 125–130 cm. long; middle of the upper internode 2–2·5 mm. in diameter, hollow, with thick walls.

Inflorescence: 9·5–10 cm. long; rachis tough; each internode 5 mm. long, 2–3 mm. wide; surface glabrous; the margins fringed with short hairs; frontal tuft absent or small.

Spikelets: 21, each 12–13 mm. long, 4-flowered, 2–3 flowers fertile; rachilla hairy.

Empty glume: white, glabrous, 8 mm. long, 3 mm. across the face; keeled from apex to base, keel tooth 3–4 mm. long, lateral tooth absent; the empty glumes widely separated.

Flowering glume: glabrous, 10 mm. long, 9–10-nerved; awn 6–8 cm. long.

Hybrid, *A. ovata* ♀ × *T. vulgare* var. *erythrospermum* ♂ (*A* × *F*, Plate II).

Culm: 80 cm. long; middle of the upper internode 2–2·3 mm. in diameter, nearly solid.

Inflorescence: 8–8·5 cm. long; disarticulation as in *A. ovata*; rachis tough; each internode 9 mm. long, wedge-shaped, 5 mm. across the apex, 3 mm. across the base; frontal tuft absent.

Spikelets: 11, 12 mm. long, 5-flowered, sterile.

Empty glume: white, glabrous, 10 mm. long, 4–5 mm. across the face, with 6–7 strong ribs, including the prominent keel which extends from apex to base; 3 ribs more pronounced than the rest; awns 2, of different lengths on each glume, those of the lower spikelets 1 and 1·7 cm. long, of the upper spikelets 2·5 and 5 cm. long respectively.

Flowering glume: glabrous, 6-nerved, with one awn, 7–8 cm. long. Long scattered hairs on the leaf blades, auricles and margins of the leaf sheaths, as in *A. ovata*, but less numerous; plant very glaucous.

Bread Wheat, *Triticum vulgare* Host. var. *albidum* Körn. (Starling form).

Culm: 120–130 cm. long; middle of the upper internode 3 mm. in diameter, hollow.

Inflorescence: 7·5–8·5 cm. long; rachis tough; each internode 3 mm. long, 3 mm. wide at the apex, 2 mm. across the base; margins fringed with short hairs; frontal tuft small.

Spikelets: 22–24, each 13 mm. long, 4-flowered, 3–4 flowers fertile.

Empty glume: white, glabrous, 9 mm. long, 4 mm. across the face; keeled only slightly in the upper half; apical tooth 1 mm. long, blunt; the two empty glumes widely separated.

Flowering glume: quite glabrous, 10 mm. long, 9–10-nerved, with a tooth or awn 1–2 mm. long in the lower, 7–9 mm. long in the upper spikelets.

Hybrid, *A. ovata* ♀ × *T. vulgare* var. *albidum* ♂.

Culm: 75–80 cm. long; middle of the upper internode 2·5 mm. in diameter, hollow.

Inflorescence: 8–8·5 cm. long; disarticulation as in *A. ovata*; rachis very tough; each internode 7 mm. long, 3·5–4 mm. across the apex, 2 mm. across the base; margins fringed with short hairs; frontal tuft small.

Spikelets: 11–13, each 13–14 mm. long, one or two lowest rudimentary, the rest fully developed with 5 flowers, all sterile.

Empty glume: very tough, white, glabrous, 10 mm. long, 4 mm. across the face, with 7 ribs and slight keel; usually 3 short teeth at the apex, the keel tooth 2 mm. long in the lower, 4 mm. long in the upper spikelets; the margins of the empty glumes meet but do not overlap.

Flowering glume: glabrous, 10 mm. long, 3–5-nerved; awns of the glumes of the lower spikelets 3–5 mm. long, of the upper spikelets 20–25 mm. long.

On the leaf blades, auricles and margins of the lower leaf sheaths are a few long hairs. The whole plant much more glaucous than either parent.

Bread Wheat, *Triticum vulgare* Host. var. *milturum* Körn. (Solino d'Ascoli, Spain) (*G*, Plate II).

Culm: 125 cm. long; middle of the upper internode 3 mm. in diameter, hollow with thick walls.

Inflorescence: 9 cm. long; rachis tough; each internode 5 mm. long, 3 mm. wide; margins fringed with hairs; frontal tuft short.

Spikelets: 18, each 13–15 mm. long, 4–5-flowered, 2–3 flowers fertile; rachilla hairy.

Empty glume: pale red, glabrous, 10 mm. long, 4 mm. across the face; keel not prominent, ending in a short, blunt tooth, ·8–1 mm. long; the empty glumes widely separated.

Flowering glume: glabrous, 11–12 mm. long, 9–11-nerved; awn 3–7 mm. long, curved.

Leaf blades and *leaf sheaths* nearly glabrous.

Hybrid, *A. ovata* ♀ × *T. vulgare* var. *milturum* ♂ (*A* × *G*, Plate II).

Culm: 65–85 cm. long; middle of the upper internode, 2·5–3 mm. in diameter, hollow with thick walls.

Inflorescence: 9–10 cm. long; disarticulation as in *A. ovata*; rachis very tough; each internode 7 mm. long, wedge-shaped, 3·5 mm. across the apex, 2 mm. across the base; margins fringed with hairs; frontal tuft short.

Spikelets: 14, each 15 mm. long, 5-flowered, sterile; rachilla hairy.

Empty glume: pale red, glabrous, very tough, 12 mm. long, 5 mm. across the face; keel not prominent; two short lateral teeth and a keel tooth, the latter on the lower glumes 1 mm. long, on the upper glumes 5 mm. long; the empty glumes meet but do not overlap.

Flowering glume: 11–13 mm. long, 3–5 nerved, glabrous, with one awn, which on the lowest spikelets is 3 mm. long, on the upper spikelets 25 mm. long.

Leaf blades: with scattered long hairs on the upper surfaces, and ciliate margins to the lower leaf sheaths as in *A. ovata*. The whole plant more glaucous than either parent.

From a superficial inspection of these hybrids it is generally concluded that the wheat characters are dominant, but that this is not the case is soon discovered when each of the characters of the parents and the crosses is critically examined and compared.

The majority of the characters of the hybrids are intermediate, or a visible blend of those of the parents.

Taking the various characters *seriatim* the following conclusions are established.

Culm. In regard to the total length of the culm and the diameter of its upper internode the hybrids are intermediate between those of the parents.

In those cases in which the wheat parent has a solid upper internode the internode of the hybrid is hollow, but with much thicker walls than those of the *Aegilops* parent.

Inflorescence. In number of spikelets and length of the internodes of the rachis the hybrids are intermediate.

The total length of the inflorescence of the hybrids is very nearly the same as that of the wheat parent, and twice as great as that of the *Aegilops*. This apparent dominance of the wheat parent is, however, illusory, for the length of ear is dependent upon the number and length of the internodes, in which two characters the hybrids are intermediate.

The width of the internodes of the rachis is slightly larger in the hybrids than in either parent.

The peculiar mode of disarticulation of the ear from the culm in *Aegilops* is a dominant character; all the hybrids with *durum* and *vulgare* wheats in which it is absent show it, and so far as can be estimated, in a degree equal to that of the *Aegilops*.

The fragility of the rachis of the Wild Emmer is dominant over the tough rachis of *Aegilops*, the ears of the hybrids separating at the rachis nodes almost as readily as the Emmer parent; but in the case of the hybrid with the fragile-eared Abyssinian Emmer there is evidence of the influence of the tough rachis of the *Aegilops*, for the hybrid ears do not break quite so readily at the nodes as those of the Emmer parent.

Glumes. (1) *Flowering glumes.* The flowering glume of *Aegilops ovata* possesses two awns and a small tooth, that of wheat only one awn; the hybrids have only one awn but the projecting parts of the divided apex of the glumes are slightly longer than those of the wheat parent, which they otherwise closely resemble.

In hybrids between *Aegilops* and the bearded Emmer and Macaroni Wheats, which have long awns on the flowering glumes, the number and length of the awns and number of the nerves of the glumes are intermediate. When a bearded Bread Wheat is one of the parents the hybrid has awns as long as those of this parent.

In the hybrids with a beardless Bread Wheat as one of the parents, the number of the nerves and the length of the awns on the flowering glumes are distinctly less than either parent, or only just equal to that of the *Aegilops*.

(2) *Empty glumes.* The empty glumes of the hybrids are somewhat longer than those of either parent, with a broad apex intermediate between the two parents. They are boat-shaped like those of the wheats, with a more or less obvious keel. The prominence of the keel is intermediate, and the characteristic strong ribs of the *Aegilops* are seen on the outer face of the empty glumes of the hybrids, but intermediate in number and less clearly defined.

In respect of awns on the empty glumes the inheritance is peculiar. The empty glume of *Aegilops* has four long awns and a rudimentary fifth, the wheats having only a short keel tooth at the apex of the glume.

The empty glume of the hybrids in which a wheat with a long awn on the flowering glume is one of the parents, has two awns and a short tooth between them; the awns are of different lengths, the longer being considerably longer than those of *Aegilops*, and two or more times as long as the shorter one.

The empty glume of the hybrids in which a beardless Bread Wheat is one of the parents, possesses three short teeth, namely, a keel tooth 1–5 mm. long, and two lateral teeth ·5–2 mm. long, the middle one being the shortest.

While the number of the awns or teeth on the empty glumes of the hybrids is intermediate between that of the two parents, the presence or absence of long awns on these *empty glumes* is determined by the presence or absence of awns on the *flowering glumes* of the wheat parent, whose empty glumes are awnless.

The great majority of wheats of all races have awnless empty glumes, and the rare cases in which these glumes are awned are found, so far as my experience goes, chiefly among the Bread Wheats and allied Club Wheats; this, together with the fact that in these hybrids with *Aegilops ovata* the empty glumes are awned, lends support, I think, to the view I have expressed elsewhere, that the Bread Wheats are hybrids into whose constitution *A. ovata* has entered.

Colour of empty glumes. In the cross between *Aegilops* with its pale straw-coloured glumes and *T. dicoccoides* var. *spontaneonigrum* in which the empty glumes are black, the glumes of the hybrid are reddish with small black stripes and spots.

Hairs. In length and number of hairs on the leaf blade, leaf sheath and rachis the hybrids exhibit a blend of the two parents.

CYTOLOGY.

Investigations were carried out upon the segregation of the chromosomes in the divisions of the microspore mother-cells, and tetrad and microspore formation in two of these *Aegilops* × Wheat hybrids; chromosome counts have also been made during several seasons of representatives of all the species and races of wheats, and six species of *Aegilops*.

Method. Young inflorescences still hidden in the upper leaf sheath are removed, and the internode of the rachis severed between each spikelet. The separate spikelets are then cut transversely across their bases, after which, individual flowers can be easily obtained free from the glumes.

A single anther is taken and mounted in a drop of Belling's aceto-carmine; a thin cover is placed on this and a very gentle vertical tap is given with the point of a needle. With the right pressure the complete column of undamaged microspore mother-cells bursts out of the anther. The edge of the coverslip is slightly lifted for a short time to allow plenty of stain to reach the cells, and in one or two minutes the nuclei are stained deeply and in cells undergoing division the chromosomes stand out conspicuously, and counts are easy and certain.

By this method, and using only a single anther, the various stages in the division of the microspore mother-cells can be rapidly determined, after which the remaining two anthers of the same flower, which are usually in the same phase of development, may be fixed and kept for extended study. In this manner only anthers containing actively dividing cells need be fixed, and the useless labour and annoyance of fixing, cutting and staining large amounts of material unsuited for the study of mitosis is entirely avoided.

The fixing solutions used in these studies were acetic alcohol (1 : 3) and weak chromo-acetic mixture. For all stages up to the completion of the heterotype and following homotype divisions acetic alcohol gives good results, but for the later phases of microspore development this solution produces serious shrinkage, and chromo-acetic or weak Flemming is better.

Haidenhain's iron-haematoxylin stain was used, and the sections cut 12–14 μ thick; complete mitotic figures were not often obtained in sections much thinner than this. Both longitudinal and transverse sections were cut, the former being of most service in elucidating the irregular mitotic figures found in these hybrids.

The following are the chromosome numbers found in the species and races of wheats mentioned:

Diploid. $x=7$	Tetraploid. $x=14$	Hexaploid. $x=21$
T. aegilopoides var. *boeoticum* var. *Larionowi*	*T. dicoccoides* var. *Aaronsohni* var. *spontaneonigrum*	*T. vulgare*, 25 forms
T. monococcum var. *vulgare* var. *flavescens*	*T. dicoccum* var. *Ajar* var. *farrum*	*T. compactum* var. *erinaceum*
	T. orientale var. *notabile*	*T. sphaerococcum* var. *tumidum*
	T. durum var. *affine* var. *hordeiforme* var. *australe*	*T. Spelta* var. *album*
	T. polonicum var. *levissimum*	
	T. turgidum var. *iodurum* var. *lusitanicum*	
	T. pyramidale var. *recognitum*	

These determinations are confirmatory of the observations of Kihara (6), Sakamura, Sax and others in regard to the wheats examined by them, and establish the numbers for varieties of *T. aegilopoides*, *T. dicoccoides*, *T. orientale*, *T. pyramidale* and *T. sphaerococcum* hitherto unexamined.

In the genus *Aegilops* (which is placed by many systematists in the genus *Triticum*) the basic chromosome number is the same as that of the wheats, namely seven, and I find diploid, tetraploid and hexaploid species in the genus as in the wheats.

The following are the species of *Aegilops* examined and their chromosome numbers:

Diploid. $x=7$	Tetraploid. $x=14$	Hexaploid. $x=21$
A. squarrosa L.	*A. ovata* L.	*A. crassa* Boiss.[1]
A. speltoides Tausch.	*A. triuncialis* L.	
	A. ventricosa Tausch.	

Kihara (6) gives the $2x$ number as 28, for *A. ovata*, *A. ventricosa* and *A. squarrosa*. Since the nomenclature of some of the species of *Aegilops* is extremely involved, it is absolutely essential that the authority should always be quoted with each name when referring to plants of this genus used in genetic investigations, or confusion is certain to arise. In this connection it is not out of place to note that the name *Aegilops cylindrica*

[1] A form with awned empty glume grown at Reading for some years, originally from Transcaspia, and sent by the Bureau of Applied Botany, Leningrad; typical forms from Turkestan have fourteen as the haploid number.

has been given by systematists to three or four different species. Similarly the name *A. squarrosa* has been applied to the European species *A. ventricosa* Tausch., *A. caudata* L. and *A. cylindrica* Host., as well as to the Asiatic *A. squarrosa*.

The pentaploid hybrid, *A. ovata* ♀ × *T. vulgare* (Starling) ♂.

The pre-synaptic changes in the nuclei of the microspore mother-cells were not critically examined.

In synizesis the nucleus shows the usual dense knot from which emerges comparatively thin spireme threads, some of which are parallel pairs (Fig. 1). The threads soon become segmented and after condensation appear in diakinesis as short compact chromosomes of approximately equal length. No clear examples of diakinesis were observed in which the total diploid number of chromosomes could be counted with certainty, but in many nuclei at this stage both bivalents and univalents were present, the components of the bivalents lying side by side (Fig. 2).

On the bipolar spindle which soon appears the chromosomes become shorter and denser with a clean-cut outline, and are easily counted with certainty. The diploid number in this hybrid was found to be 35 as expected (Figs. 3, 4, 5), 21 being received from the wheat, and 14 from the *Aegilops* parent.

In the majority of cells the metaphases of the heterotype division exhibit the diploid number of univalents irregularly distributed on the spindle, often with some in the cytoplasm away from it. Close pairing of the chromosomes into typical bivalents was not seen, and no cell was observed in which all the chromosomes were collected on a definite equatorial plate, the nearest approach to this being given in Fig. 5.

In the anaphases there is considerable irregularity in the movement of the univalents towards the poles, 5 to 7 usually reaching each pole, while the rest are still in the equatorial zone of the cell. Moreover, almost as soon as the anaphase begins most of the chromosomes undergo a longitudinal division, as in Fig. 6, but a small number generally remain undivided, more especially the few which lie outside the spindle or which have taken up their position near the pole immediately after diakinesis. The appearance in Fig. 7 in which are seen four groups of chromosomes, two at the poles and two moving towards this position, is characteristic of the heterotype division in this pentaploid hybrid; the presence of undivided univalents—in Fig. 7 there are 3 or 4—along with homotypically divided univalents is also characteristic of this phase of meiosis.

Complete details of the telophases of the heterotype division were not provided in the material investigated, but tetrads produced by sub-

sequent divisions showed the mother-cell divided into 2–6 cells in which were present large nuclei of irregular form and structure, often accompanied by dwarf nuclei containing from 1–3 chromosomes. I have not been able to trace completely the origin of these dwarf nuclei, but observations show that they are formed around univalents which never divide either in the heterotype or homotype divisions of the mother-cell, or only do so at a very late period of the final mitosis.

Four microspores normal in form and size are sometimes produced from a single mother-cell, but in the majority of cases cleavage furrows divide the cytoplasm into an irregular and larger number of microspores of several different sizes (Figs. 9–11).

Frequently the cleavage furrows extend inwards some considerable distance across the dividing cell before the division of the nucleus is concluded, and sometimes the furrows remain uncompleted, in which cases twin microspores result as in Fig. 10.

In the tetrad divisions minute portions of cytoplasm, which appear to contain no chromosomes at all, are sometimes cut off, but no matter what the size of the daughter-cells, the thick extine of the pollen grain is completely formed, and in all, except possibly the most minute grains, the characteristic pore is developed (Fig. 11); occasionally two germ pores are present (Fig. 10).

Some of the microspores in completely ripe anthers contain neither cytoplasm nor nucleus; others appear normal and possess two typical gametic nuclei which stain intensely with aceto-carmine but vegetative nuclei, if present, are not revealed with the same stain (Fig. 12).

The tetraploid hybrid, *A. ovata* ♀ × *T. dicoccum* var. *Ajar* ♂.

In this hybrid the diploid number was found to be 28 as expected, namely, 14 from each parent.

Although the number of chromosomes from each parent is the same, the bivalents are only loosely paired in the metaphase of the heterotype division, and I found no cells in which all the chromosomes were collected on a clearly defined equatorial plate. Movement of the chromosomes towards the poles from the metaphase position is generally irregular, from 5 to 7 pairs of the chromosomes frequently completing their anaphase before the remainder have begun to leave the equatorial plate (Figs. 13–18).

As in the pentaploid hybrid, the homotypic split is visible in some of the separated univalents very soon after they reach the poles of the heterotype spindle, and in some cases before attaining this position;

other univalents remain undivided for some time and have a tendency to lag behind the rest or wander off the spindle.

The movement of the chromosomes towards the poles of the heterotype spindle in two groups leaves its impress on the telophases of this division, for the first group of univalents to reach the poles enter the telophase in advance of the second group, and in the majority of cases two or more separate nuclei are formed at each pole (Figs. 20, 21), these nuclei being irregular in form and containing a variable number of chromosomes. In some divisions one or more chromosomes lag behind and never become associated with their neighbours.

In the succeeding homotype division and tetrad formation is seen a similar movement of the divided chromosomes in two groups travelling to the poles at different rates (Figs. 22, 23).

Irregular telophases follow with the formation of microspores, within which are two or more nuclei usually of different sizes and containing a variable number of chromosomes (Fig. 24).

In only a very small proportion of the mother-cells does the division proceed in such a manner as to result in the production of a typical 4-celled tetrad (Fig. 26); in the great majority lagging of the chromosomes occurs in both the heterotype and homotype divisions, and the tetrads ultimately formed consist of 5 to 7 or more cells, each with a nucleus of variable chromosome constitution (Figs. 25, 27).

The chromosomes of *Aegilops* and those of the wheats are indistinguishable; it is therefore not possible to determine whether the loose pairing which occurs in the heterotype division takes place between homologous chromosomes derived from both parents, or between chromosomes from the same parent.

In the pentaploid hybrids investigated by Sax (7), Kihara (6), Watkins (9) and others, resulting from the hybridisation of a wheat of the Emmer series possessing 14 chromosomes, and a Bread Wheat having 21 chromosomes, it is concluded that each bivalent consists of a chromosome from each parent. In such hybrids 14 from one parent unite with 14 from the other, leaving 7 univalents unpaired, the latter remaining near the equatorial plate in the heterotype division after the components of the bivalents have separated and moved to the poles of the spindle in the normal manner.

In the pentaploid hybrid between *Aegilops ovata* and a Bread Wheat similarly involving 14 and 21 chromosomes respectively, there are almost invariably two groups of separating chromosomes in the heterotype division, as in pentaploid wheat hybrids, but the larger number, which

is always much nearer 21 than 7, is found in the equatorial zone. This observation suggests the probability that such pairing as occurs in this case takes place among the 14 *Aegilops* chromosomes, and that these separate and reach the poles before the more numerous wheat chromosomes move far from the metaphase position.

In the tetraploid hybrid between *Aegilops ovata* and Emmer Wheat in which an equal number of chromosomes, namely 14, are supplied by each parent, on the assumption that pairing takes place between homologous chromosomes from each parent, it might be expected that all the bivalents would be oriented on a well-defined equatorial plate, since qualitatively they would be all alike; further, in the anaphase 14 chromosomes should travel to each pole at the same time leaving none on the equatorial plate. This, however, is not the case in the example investigated. Although pairing here is loose, and there are certain irregularities in the mitoses, the chromosomes of the heterotype division are arranged in two groups, approximately 14 in each, one group travelling to the poles of the spindle, while the other, in the form of 7 loosely associated bivalents, are still in metaphase. If the bivalents were qualitatively all alike, as they should be if each is composed of homologous chromosomes from both parents, it would be expected that the separating components in the anaphase would travel simultaneously to the poles of the spindle and not in two groups. That the movement occurs in two groups I take to be evidence that the bivalents concerned are qualitatively unlike, and that the 7 bivalents loosely paired on the equatorial plate consist of pairs of wheat chromosomes, the others moving to the poles earlier being *Aegilops* chromosomes, or *vice versa*. The fact that the number which first reaches the poles in the pentaploid hybrid is small (from 5 to 7) suggests that these belong to the *Aegilops* parent, the larger number remaining near the equatorial zone being wheat chromosomes.

Sterility in these hybrids is doubtless to be attributed to the great irregularity in the tetrad and microspore formation.

Bally (2) studied the cytology of a pentaploid hybrid between *Aegilops ovata* and *Triticum vulgare* similar to that just described. He gives the haploid chromosome number of *A. ovata* as 16, that of the wheat as 8; both numbers are incorrect and the conclusions based upon these figures are consequently valueless. He observed, nevertheless, double threads arising from the synaptic knot, bivalents and univalents at diakinesis, the absence of a typical metaphase, the movement of the chromosomes at two different rates in the heterotype division showing some in ana-

phase with others in metaphase in the same cell, from 3 to 5 undivided chromosomes at the poles with undivided chromosomes just leaving the equatorial plate, and the formation of irregular tetrads and microspores; in all these points my investigations agree with those of Bally.

More recently Sax (8) has given an account of the cytology of a cross between *A. cylindrica* and *T. vulgare*. He gives the haploid number of the *Aegilops* as 14, that of the wheat as 21; the chromosome numbers involved in his hybrid are, therefore, the same as those of the hybrid of *A. ovata* and *T. vulgare* dealt with in this paper.

Both paired and unpaired chromosomes were seen at diakinesis, and in the metaphase of the reduction division he reports the presence of 7 bivalents and about 21 univalents. Lagging of univalents and equational division in the heterotype division occurs, and, although extra nuclei are sometimes produced, tetrad formation is comparatively regular.

SUMMARY.

1. Hybrids were obtained between *Aegilops ovata* and several forms of four different races of wheat, namely, *Triticum dicoccoides*, *T. dicoccum*, *T. durum* and *T. vulgare*, the mother parent being *A. ovata*. The reciprocal crosses were unsuccessful.

2. All the hybrids were sterile.

3. In respect of the following characters, the hybrids were intermediate, *i.e.* a blend of both parents; amount of pith and diameter of the upper internode; number of spikelets in the ear; length of the internodes of the rachis; number of nerves and number of awns on the flowering glumes in those cases in which the Emmer and Macaroni wheats were parents; colour of chaff; pubescence of the leaf blade, leaf sheath and rachis; and prominence of the keel on the empty glumes.

4. In length of awn of the flowering glume, the hybrids closely resemble the Bread Wheats when these enter into the cross.

5. The number of awns on the empty glumes is intermediate, but long awns are only obtained on the empty glumes when the wheat parent has long awns on the flowering glumes; empty glumes of the hybrids possess only short teeth when a beardless Bread Wheat, with very short awns on the flowering glumes, is a parent.

6. Empty glumes of the hybrids are longer than those of either parent.

7. The only dominant characters observed were fragility of the

rachis of the wild Emmer, and the mode of disarticulation of the inflorescence of the *Aegilops* parent.

8. The basic chromosome number in *Triticum* and *Aegilops* is 7, with similar polyploid species, $2x$, $4x$ and $6x$.

9. In both the pentaploid and the tetraploid hybrids investigated, pairing of the chromosomes in metaphase of the heterotype division is loose, and longitudinal division of the chromosomes frequently occurs soon after the univalents begin their movement towards the poles of the heterotype spindle.

10. In these *Aegilops* × wheat hybrids the chromosomes pass to poles of the spindle in both the heterotype and homotype divisions in two groups, one of them lagging behind the other. Many examples of similar behaviour of the chromosomes are known among hybrids in which the chromosome numbers of the two parents differ, but I am not aware that it has been previously observed in any hybrid between parents possessing the same number of chromosomes.

It is suggested that in these hybrids the loose pairing takes place between univalents derived from the same parent, and not between homologous chromosomes from both parents.

11. Tetrad formation is generally very irregular, and microspores of several different sizes are produced, some of which when fully developed are empty, others containing two or more nuclei with variable numbers of chromosomes; twin microspores are also produced. Sterility of the hybrids is doubtless connected with these irregularities.

12. No matter what the size of the microspores, each possesses a typical thick extine which in the majority of cases is furnished with the characteristic germ pore.

13. The microspore mother-cells of the pentaploid hybrid are of larger diameter and volume than those of the tetraploid hybrid.

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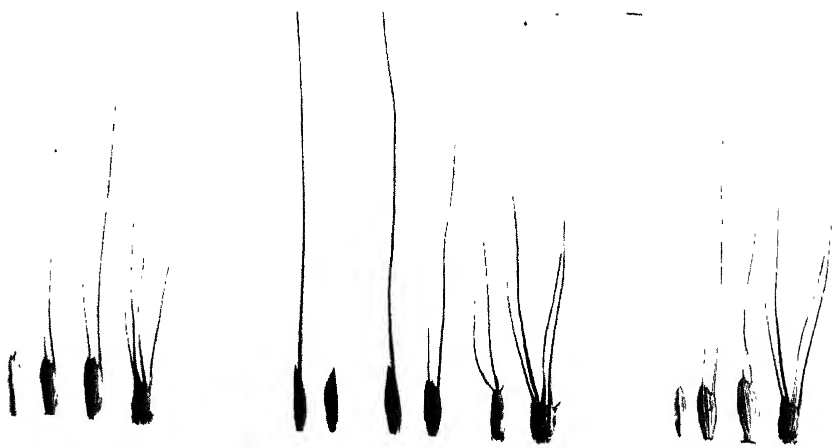
A *A* × *B* *B* *A* × *C* *C* *A* × *D* *D*



b *a* × *b* *a* *c* *a* × *c* *a′* *d* *a* + *d* *a*

A   *A×E*   *E*   *A×F*   *F*   *A×G*   *G*

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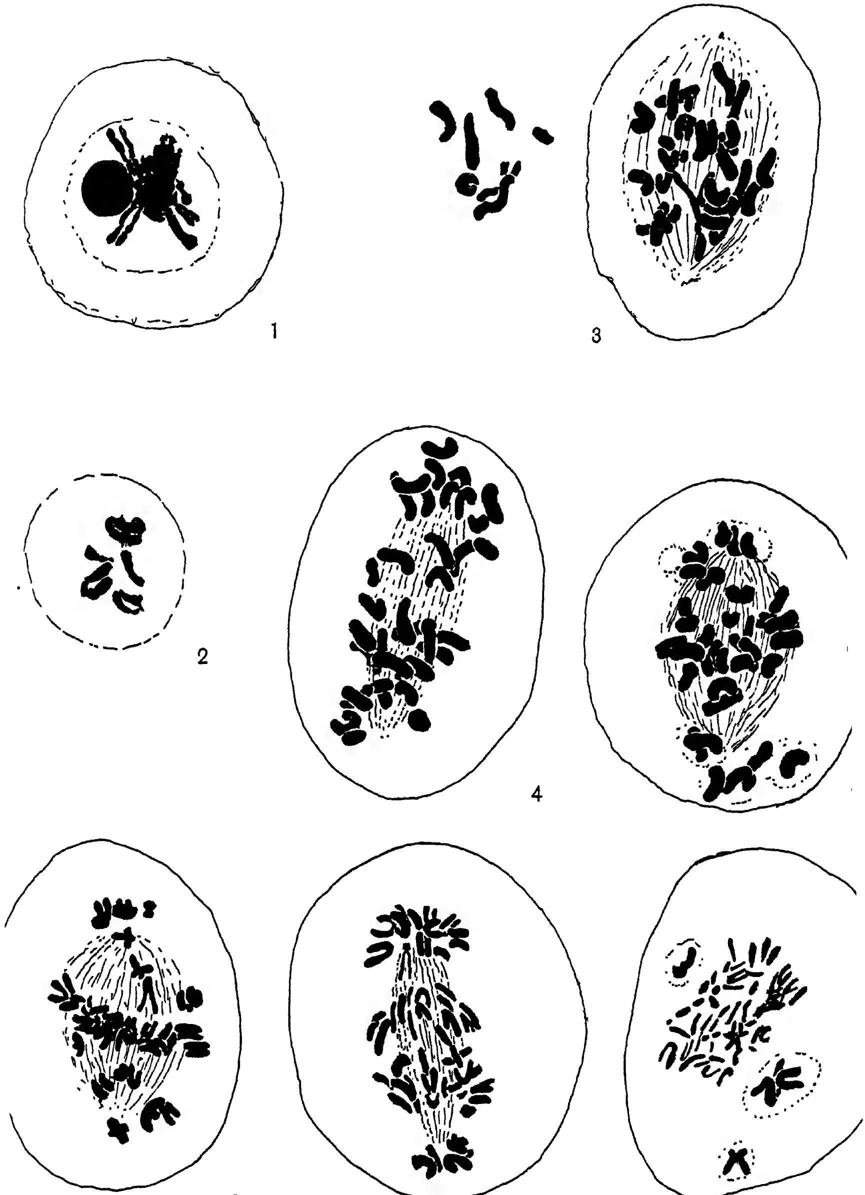

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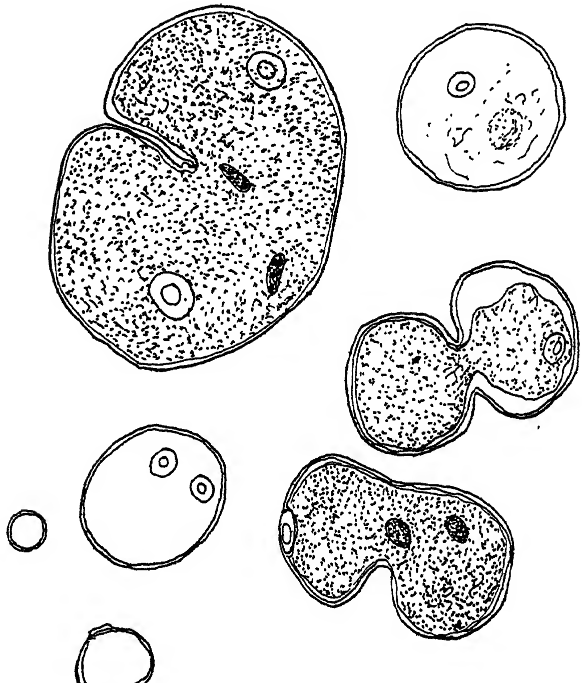

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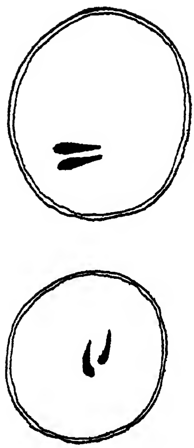

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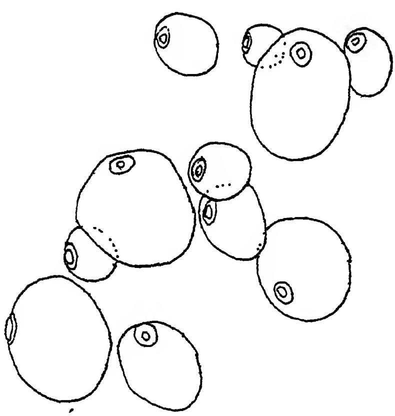

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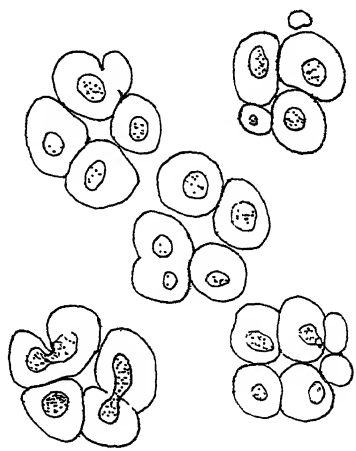

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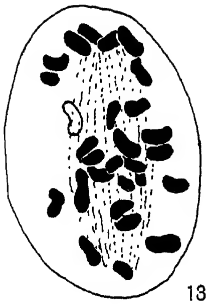
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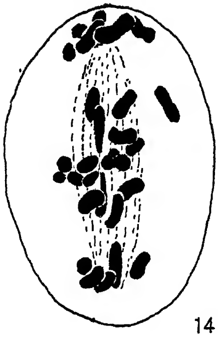
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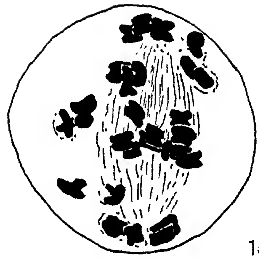
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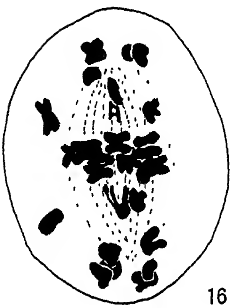
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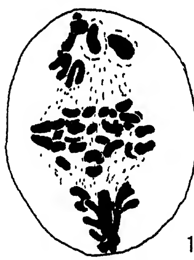
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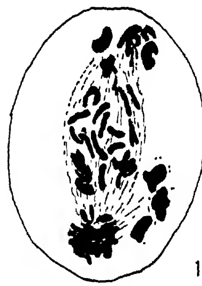
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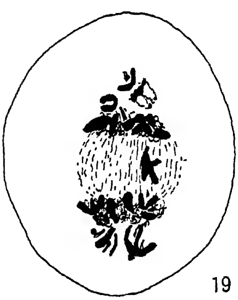
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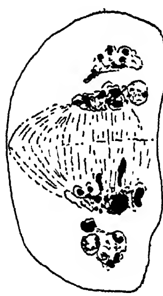
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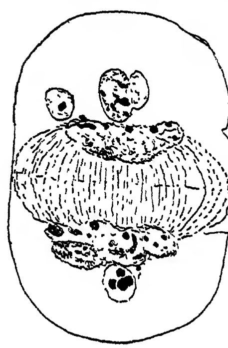
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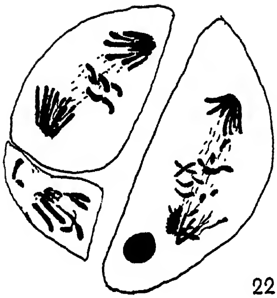

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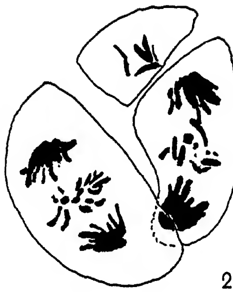

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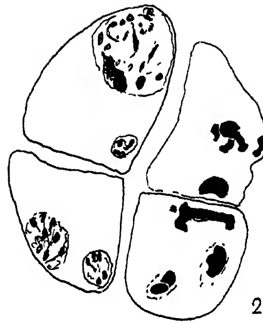

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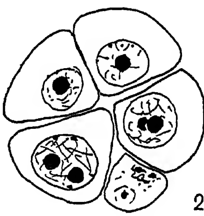

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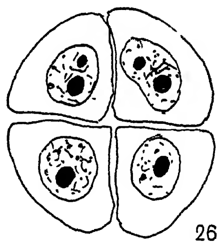

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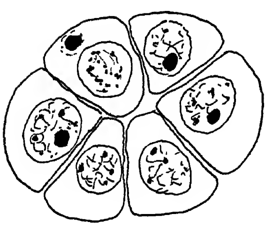

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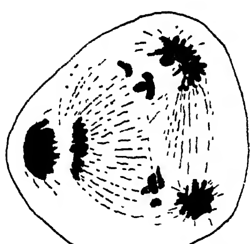

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EXPLANATION OF PLATES II—VI.

PLATE II.

(All about ⅔rds natural size.)

A, *Aegilops ovata*; *B*, *T. dicoccoides* var. *Kotschyanum*; *C*, *T. dicoccoides* var. *spontaneonigrum*; *D*, *T. dicoccum* var. *Ajar*; *E*, *T. durum* var. *affine*; *F*, *T. vulgare* var. *erythrospermum* (Greek form); *G*, *T. vulgare* var. *milturum* (Solino d'Ascoli).

$A \times B$: $A \times C$: $A \times D$: $A \times E$: $A \times F$: $A \times G$: hybrids. *A* in all cases the ♀ parent.

a, *b*, *d*, *e*, *f*, empty glumes of *A*, *B*, *D*, *E*, *F* respectively.

a′, *c*, empty glume and flowering glumes of *A* and *C* respectively.

g, empty glume and two flowering glumes of *G*.

$a \times b$; $a \times d$; $a \times e$; $a \times f$, empty glumes from upper and lower spikelets of hybrid ears.

$a \times c$, empty glume and flowering glume of $A \times C$:.

$a \times g$, two empty glumes and two flowering glumes from upper and lower spikelets of hybrid $A \times G$.

PLATES III—VI.

All the figures are drawn with the aid of Abbe's camera lucida and are from single sections, with the exception of 3 and 13; Zeiss' apochromat 2 mm. objective and No. 12 ocular.

Figs. 1–8, 10, 12–28, magnification 1000 diameters, reduced in reproduction to 800 diameters; Figs. 9 and 11, magnification 400 diameters, reduced to 320 diameters.

I. Pentaploid hybrid, *A. ovata* ♀ × *T. vulgare* var. *albidum* (Starling) ♂.
Divisions of microspore mother-cells.

Fig. 1. Double spireme and chromosomes appearing from the synaptic knot.

Fig. 2. Portion of nucleus in diakinesis.

Figs. 3, 4, 5. Metaphases of heterotype division.

Figs. 6, 7, 8. Heterotype divisions; most chromosomes longitudinally divided in anaphase and metaphase.

Fig. 9. Irregular tetrads; some cleavages incomplete, nuclei of irregular size and form. (Fresh material stained with aceto-carmine.)

Fig. 10. Single and twin microspores. (Fresh material stained with aceto-carmine.)

Fig. 11. Microspores from ripe anther. (Unstained.)

Fig. 12. Two fully developed microspores from the same anther as those of Fig. 11. (Stained with aceto-carmine.)

II. Tetraploid hybrid, *A. ovata* ♀ × *T. dicoccum* var. *Ajar* ♂.

Figs. 13–18. Profiles of heterotype spindles; in 14–18 chromosomes in anaphase and metaphase, with divided and undivided univalents present in 15–18.

Figs. 19–21. Telophases of heterotype division.

Figs. 22–23. Homotype division before completion of tetrads; chromosomes in anaphase and metaphase.

Fig. 24. Telophases with small extra nuclei, or chromosomes in the cytoplasm.

Figs. 25–27. Regular and irregular tetrads.

Fig. 28. Mother-cell with tripolar spindle figure; chromosomes in late anaphase.

THE ANOMALOUS APPEARANCE OF MALE SEXUAL CHARACTERS IN FEMALE FOWLS[1].

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Science Research Scholar of the Royal Commission for the Exhibition of 1851

(With Three Plates.)

Sex-reversal was first described in birds by Boring and Pearl (3) in 1918 when they recorded, in a series of abnormal fowls, three birds which "were changing from a female to a male condition in respect to internal structure (gonads), external characters and sex behaviour." Later a series of eight sex-reversed fowls, the most remarkable of which functioned as a fertile female before, and as a fertile male after the transformation, was described by Crew (5) and Fell (6). Another case was recorded by Gatenby and Brambell (8). A fowl described by Berner (2) is probably of the same nature. These cases all occurred naturally. Benoit (1) was the first to describe an experimentally induced reversal in the fowl. He removed the ovaries from young chicks, several of which later developed testes. Caridroit and Pézard (4) achieved similar results in adult birds. Ovariotomy followed by autoplastic ovarian grafting was performed. Subsequently sex cords and spermatic tubules were found to have invaded the stroma of the grafts. Greenwood (9) and Finley (7) obtained similar results in ovarian grafts in normal and castrated male fowls.

Many workers have maintained that the head-furnishings of the male fowl are produced by a hormone formed in the testis and that hen-feathering in the female fowl is produced by a hormone formed in the ovary. This theory is borne out by the work of the two last mentioned authors. It is known that in gonadless fowls of either sex the plumage is of the male type but is looser in texture and more luxuriant in growth; in the normal hen, and in cocks, castrated or uncastrated, into which

[1] From the Depts. of Physiology and Biochemistry, and the Dept. of Embryology and Histology, University College, London. One of the birds described (T. 1) was purchased out of a grant from the Ministry of Agriculture and Fisheries (A. S. P.). The remaining birds were purchased and maintained and all the histological expenses were met by a Grant from the Government Grants Committee of the Royal Society (to F. W. R. B.).

ovarian tissue has been successfully grafted, the plumage is of the female type; in the normal male and in ovariotomised females into which testis has been successfully grafted the plumage is male in type.

This appears to show that the ovary invariably inhibits the development of male-feathering and produces hen-feathering, and that the testis invariably produces the development of the male head-furnishings. Conversely we should expect that male-feathering can never occur with a functional ovary, nor male head-furnishings with absence of testis. Hen-feathering is sometimes found in all the males of certain breeds and occasional males in other breeds, but if the testes are absent or removed they develop plumage of the typical capon type. This does not damage the theory as it is easy to assume that the testes of these hen-feathered males have the same effect as an ovary on the plumage and at the same time the normal testicular effect on the head-furnishings.

The five birds described in this paper are of interest in this connection. The first was a functionally active female with complete male plumage. The second was possibly a case of sex-reversal. The remaining three were females with male head-furnishings, and no trace whatever of testicular tissue. Four of the five birds are in discordance, therefore, with the above-mentioned theory.

All the birds, after they came into our possession, were photographed and kept under observation for several months. If there was any apparent change in the external characters during this period they were photographed again. They were killed and dissected, and the reproductive organs photographed *in situ*. The gonads and other endocrine organs were fixed as soon as possible. In each case the gonad was cut serially and sections taken from the ribbon at frequent intervals were mounted and examined. Almost all of each gonad was fixed in Bouin's fluid, only minute portions being fixed in Champy's fluid.

T. 1. This bird was said to have been hatched in May, 1923. It was a White Leghorn, but not pure bred, and was said to be hen-feathered until November, 1923, when male plumage, with a few black feathers on the saddle, and spurs developed. It was further stated that it did not lay, was never heard to crow nor was ever seen to tread the other hens. This bird came into our possession in September, 1924, and was then apparently in good health. The plumage was as described. The spurs were well developed, but the comb and wattles were like those of a hen. It clucked like a hen, did not court the other hens, nor was courted by the cock. This bird started to lay in the first week of December, 1924,

and was then mated with a well-bred Light Sussex male, and the eggs were hatched. A trap-nest was used to avoid all chances of mistake. Four of the eggs were fertile and hatched out. The four chicks were almost entirely black when in down. Three of them died when small and proved on dissection to be two males and one female. The fourth grew to maturity and proved to be a female. All four offspring were apparently normal in every way.

The parent bird ceased laying and started to moult in February, 1925, and in March, 1925, was still completely male-feathered, but had lost the black feathers and was almost entirely white. The head-furnishings, spurs and carriage appeared to be like those of a male. Plate VII, fig. 1 *a*, is a photograph of the bird at this time. It seemed healthy, but was light to handle, and very wild. It allowed the cock to tread it, but also called hens to food as if it were a male. The cock was then separated from it. By June the moult had apparently been completed, but, between then and the end of September, a large number of black feathers were developed on the back and breast, which were retained until it was killed. The bird was mated with two pullets to which it behaved like a cock in calling them to food, but was not observed to tread them. The pullets' eggs were incubated but proved infertile. In October, 1925, T. 1 started to lay again and was in good health. Plate VII, fig. 1 *b*, is a photograph taken on 22 December, 1925, when the bird was killed and dissected. The plumage was entirely male with a large number of black feathers. The spurs and head-furnishings were well developed like those of a male. The bird clucked like a hen. Plate VIII, fig. 1, is a photograph of the dissected urogenital tract. The spleen was enlarged and tuberculous. The (left) ovary was well developed, with numerous oocytes up to 5–10 mm. in diameter. The left oviduct was also well developed. There was no trace of a gonad or oviduct on the right side. With the exception of the spleen all the organs appeared normal, and like those of a healthy hen out of the laying-period.

On histological examination the ovary was found to contain many small follicles, normal, cystic and atretic. Areas loaded with pigment granules were present. There was no trace of spermatic tissue, or undifferentiated sex-cords anywhere. In fact there was nothing abnormal about the ovary, which seemed in a state of involution typical of the ovaries of fowls just after a period of active egg-production.

T. 2. This bird, a Brown Leghorn, came into our possession in the end of May, 1925, without any previous history except that it had been

bred from good stock and had not laid an egg for two months or more. The plumage was female in type, but the head-furnishings were like a male, well developed and erect. Plate VII, fig. 2, is a photograph taken at this time. Spurs were absent. The bird weighed 2200 grm. The cock called her and attempted to tread her. This bird was killed and dissected on 15 December, 1926. At this time its weight had dropped to 1700 grm., but the bird appeared healthy. Plate VIII, fig. 2, is a photograph of the dissection of the urogenital tract. The left gonad was small, and lobulated like an ovary. No oocytes were visible, but numerous smooth cream-coloured lobules suggested the presence of testicular tissue. The left oviduct was small. There was no gonad on the right side, but a rudimentary right oviduct was present. The histological examination of the gonad of this bird showed what appeared to be an ovotestis. The ovarian regions contained many small and apparently normal oocytes. The cortex in these regions was considerably thickened, and appeared to be in an active condition. Ingrowths from the epithelium, resembling the sex-cords in the embryonic gonad, appeared to be forming. In some places groups of tubules could be found in the cortex amongst the oocytes.

The major portion of the gonad, however, was composed almost entirely of these tubules, with here and there an occasional oocyte, surrounded by its follicle, in amongst them. Plate IX, fig. 2, is a microphotograph of such a region. Some of these oocytes appeared healthy, but most of them were in more or less advanced stages of degeneration. The tubules vary in size considerably, the smaller ones being round, almost solid, cords of cells, while the larger ones had irregular outlines, like those of mature spermatic tubules cut in various directions, and large lumina. This appearance suggests that the tubules were of different ages and represented a number of successive ingrowths. Some of the tubules have a definite epithelial lining, the cells of which have brightly staining nuclei and sharply defined cytoplasm. Many of these cells exhibit mitotic figures, and the tubules appear to be healthy and growing. In these the lumen is open and large.

In other tubules, chiefly the larger ones, the nuclei of the epithelial cells are sharp and brightly staining and appear to be healthy, but do not exhibit mitosis. These cells have the entire cytoplasm whipped out, as it were, into fine threads which fill the lumina of the tubules and look deceptively like wisps of sperm-tails under the low power. Little or no cytoplasm, other than these fine threads, remains around the nuclei. While most of the tubules of this type appear healthy, some are undoubtedly degenerating, their nuclei no longer form a peripheral layer,

but have come adrift into the lumen, and both they and the cytoplasmic threads are less sharp and brightly staining. All the intermediate stages between these two types of tubules can be found. No spermatocytes can be seen in any, yet their appearance suggests that they are spermatic in character. Each has a well-marked fibrous sheath around it, like that around the normal spermatic tubule. There is little interstitial tissue between them and they are pressed close together. There is a well-developed tunica around these (spermatic) portions of the gonad.

T. 3. This bird, an Ancona, came into our possession in May, 1925, when it was said to be three years old. It was known to lay and was never seen to tread hens or receive attention from the cocks. It crowed perfectly. The plumage was entirely female, but the head-furnishings were male in character and very well developed. The weight was 1800 grm. The spurs were rudimentary. Plate VII, fig. 3, is a photograph of the bird at this time. This bird had every appearance of being a true case of sex-reversal. The plumage and head-furnishings remained the same and it crowed vigorously until it was killed on 15 December, 1925. The weight was then 1560 grm. The post-mortem revealed an ovary on the left side with one large cystic follicle and two tumour-like masses which proved to be large follicles in an advanced stage of degeneration. The left oviduct was small. No gonad or oviduct was present on the right side. Plate VIII, fig. 3, is a photograph of the dissection of the urogenital region. Histological examination of the gonad revealed many small oocytes, mostly healthy, in the stroma. No trace of spermatic tissue or sex-cords could be found, although a careful and systematic search was made.

T. 7. This White Leghorn was said to have been hatched in May, 1923. It was also stated that it layed regularly and well during the pullet year, but after moulting the comb straightened and it began to crow regularly every day. It was received by us on 4 June, 1925. The plumage was then completely henny, but the comb, lobes and wattles were well developed and male in character. The spurs were rudimentary. The weight was 1250 grms. It was killed on 15 December, 1925, and then weighed 1400 grm. Plate VII, fig. 4, is a photograph of the bird at this time. Post-mortem examination revealed a small ovary on the left side with a knob of tissue about 1 cm. in diameter attached to its anterior end by a short stalk. There was no gonad on the right side. The left oviduct was small and atrophic, and there was a small right oviduct. Plate VIII, fig. 4, is a photograph of the dissection of the urogenital organs. Histological

examination of the gonad revealed abundant normal follicles up to 1 mm. in diameter in the stroma. There was one large degenerate follicle, the remains of which were about 6 mm. in diameter, as well as a considerable number of small atretic follicles. The cells in many regions were heavily loaded with pigment granules. Considerable fibrosis of the tissue, especially of the walls of the vessels, was observable in some regions of the medulla. The tumour-like knob of tissue referred to is difficult to identify, but may be a benign or malignant tumour or possibly aberrant chromaffin tissue, the position in the adrenal region suggesting the latter. Careful systematic search made failed to reveal the presence of spermatic tubules or sex-cords either in the ovary or in the attached knob of tissue.

T. 8. This bird of no particular breed was presented to us in June, 1925, when about a year old, by Mrs McEnery, of Newcastle House, Co. Wicklow, to whom we wish to express our thanks. The previous history was uncertain. The plumage was henny, but with a cock's head-furnishings. Spurs were absent. It clucked like a hen when frightened and did not crow nor court the other birds and was ill-tempered with cocks and hens alike. It was killed on 1 January, 1926, when in good health and condition. The weight was then 1800 grm. Plate VII, fig. 5, is a photograph of the bird at that time. Plate IX, fig. 1, is a photograph of the dissection. The post-mortem showed two or three small tumours in the mesentery. The left ovary was small (3 cm. × 1 cm. approx.) and contained no oocytes over about 1 mm. in diameter. A tumour, about 1 cm. in diameter, was attached by a short stalk to its posterior end. There was no gonad on the right side. A vas deferens and an oviduct were both present and well developed on the left side. A small oviduct about 1 cm. long was found on the right side. The histological examination showed that the ovary contained many normal oocytes and was indistinguishable from that of a normal hen in a non-laying period. The tumour was an osteoma or, more probably, an osteosarcoma. Careful systematic search of both gonad and tumour revealed neither spermatic tubules nor sex-cords.

The five birds here described may be conveniently divided into three groups:

(1) T. 1. (2) T. 2. (3) T. 3, T. 7 and T. 8.

Of these T. 2 seems to be a typical case of sex-reversal, although spermatocytes cannot be found in it. This history implies that the bird

had previously laid. The absence of a right gonad and of vas deferentia, usually found in birds that have always been hermaphrodite, and the presence of a well-developed, though small, left oviduct indicate that the bird was originally female and that the tubules had developed in later life. In the sections the growing tubules and sex-cords, and their conformity with the original irregular outlines of the gonad, together with the presence of degenerating oocytes entirely surrounded by them, support the view that it was originally an ovary and was in process of transformation in later life. We therefore consider T. 2 to be probably a straightforward case of sex-reversal.

In several ways, T. 1 is undoubtedly the most remarkable of these birds. First it had a functional ovary, and male-feathering. The simplest explanation of the observations that castrated birds of both sexes developed male plumage, while females and males, with engrafted ovarian tissue, developed hen-feathering, is that the ovary causes the development of the hen-feathering. Likewise it is easy to believe that the testes of hen-feathered males have somehow the same influence. T. 1 is a straightforward exception to this theory and, beyond pointing that fact out, we can offer no explanation. Further, T. 1, T. 3, T. 7, and T. 8 are all similar in another remarkable characteristic. They all had well-developed male head-furnishings but no trace of spermatic tissue. The obvious explanation of the numerous observations that the male type of head-furnishings is always developed in the presence of testis and not when it is absent or removed, is that testicular tissue produces and maintains its development. Now these four birds are emphatically contrary to this explanation. We would wish to draw special attention to the fact that no right gonad was present in any of them, and that a piece of spermatic tissue in the left gonad $\frac{3}{4}$ cubic mm. in size could not possibly have passed unobserved, for the sections in our series were never more than $\frac{3}{4}$ mm. apart, and were usually not more than $\frac{1}{4}$ mm. It is therefore extremely improbable that even a much smaller piece could have escaped detection, and if it did it must have been of negligible size. Yet the head-furnishings were well developed and male in type, as our photographs show. We can only record these facts without further comment and can offer no explanation of the causes which produced them.

We are indebted to Prof. J. P. Hill, F.R.S., and Dr J. A. Murray, F.R.S., for advice and criticism. We would like to take this opportunity of expressing our thanks to Miss Steward of the University College

Farm, Reading, for keeping the first bird of this series under observation for some months, and supervising the mating and breeding experiments. Our thanks are also due to Mr F. Melville and Mr W. A. Allen for assisting us with the photography.

Summary.

1. One case of probable sex-reversal in the female fowl is described.

2. One laying hen with male plumage and head-furnishings is described. There was no testis tissue present in it.

3. Three other birds with the head-furnishings of the male, but with hen-feathering, are described, though in none of them was any testis present.

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DESCRIPTION OF PLATES VII—IX.

We are indebted to Mr F. S. Pittock for the microphotograph reproduced in Plate IX, fig. 2.

Plates VIII—IX.

The following guide letters are used:

D.F., degenerate follicles. *L.D.*, left oviduct. *R.D.* right oviduct. *O.*, ovary. *T.*, tumour. *TU.*, tubules. *OC.*, oocytes.

For further explanation see text.

PLATE VII

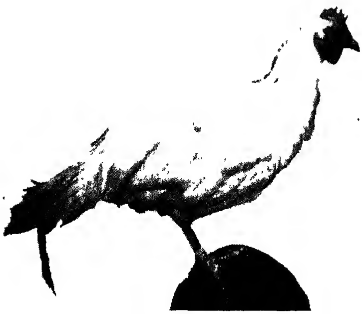


Fig. 1*a*.

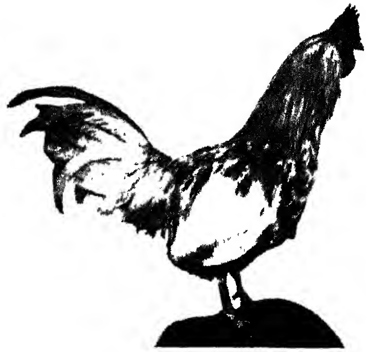


Fig. 1*b*.

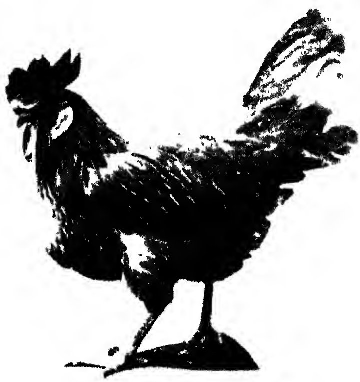


Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

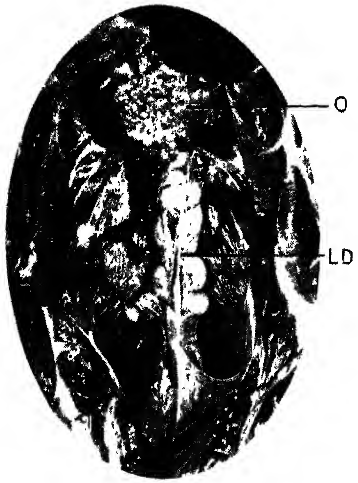


Fig. 1.

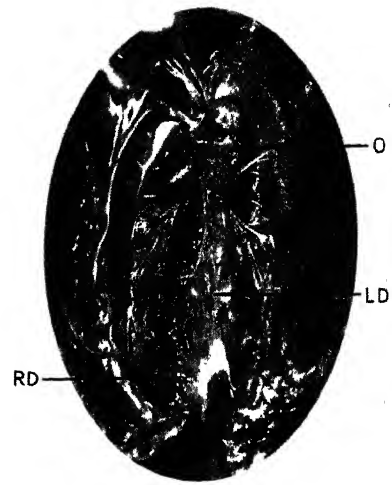


Fig. 2.

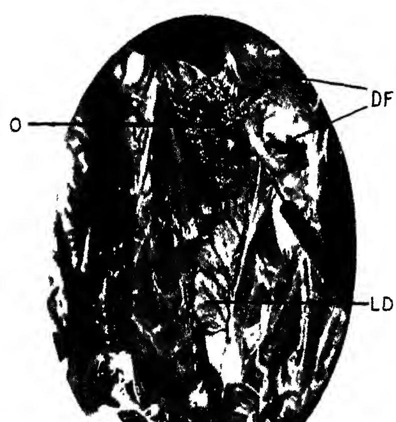


Fig. 3.

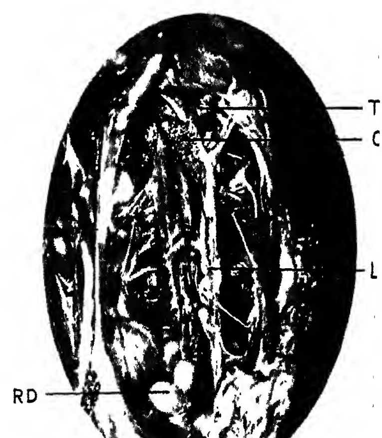


Fig. 4.

Fig. 2.

Fig. 1.

COLOUR INHERITANCE IN SHEEP. II. THE PIEBALD PATTERN OF THE PIEBALD BREED.

By J. A. FRASER ROBERTS.

From the Department of Agriculture, University College of North Wales, Bangor, and the Animal Breeding Research Department, University of Edinburgh.

(With Two Plates.)

CONTENTS.

1. *The Piebald Breed of Sheep.*

THIS ancient ornamental breed has been variously described as Spanish, Syrian, Portuguese, African, Zulu, Persian, Egyptian, Barbary, and also as "Jacob's Sheep." Owing to the uncertainty regarding the origin of the breed, it is perhaps best to follow Elwes (1913) in using the non-committal name "Piebald." These sheep possess many excellent economic qualities and it is doubtless due to this fact as well as to their picturesque appearance that so many flocks are in existence in this country, Wallace (1923) putting the number of flocks as high as one hundred and fifty.

Piebald sheep have been in existence in England for a considerable period, and pictures at Tabley House and at Wentworth painted about 1760 show that there has been little change in appearance since that time. Painstaking efforts to trace the breed in other countries have failed, and their country of origin must remain a matter of considerable doubt. There is some evidence of a North African origin, while the ease with which South African sheep imported last century were absorbed into certain flocks indicate the possibility of a relationship. A full account of his efforts to trace the history of the breed is given by Noble (1913); descriptions of the sheep will be found in the writings of Elwes (1913), Wallace (1923), Lydekker (1912), and Portal (1923), while

Plates X and XI give some idea of their appearance. Attention will be mainly confined in the present paper to the piebald pattern which is the outstanding breed characteristic. This pattern takes the form of black patches on a white ground, that is to say the black patches are usually rounded, giving an effect as though the pigment tended to spread outwards from a number of points. There is little tendency for a definite arrangement to occur, except that it is usual for the black areas to involve the two sides of the face, leaving a clear strip of white down the centre. The ewe shown in Plate XI, fig. 9, is the most typical in this respect. This arrangement, however, is not invariable.

There is wide variation in the total amount of spotting, as is shown in Plate X, figs. 1–3, and there is, perhaps, some tendency for the pigment, as it increases in total amount, to spread backwards from the forepart of the body towards the hindquarters. The nature of the spotting is also variable, in that the black patches may be comparatively small, most of the sheep illustrated in the paper coming into this category; or, on the other hand, the patches may be large, so that the pattern consists of just a very few extremely large patches spreading over the whole body. An excellent example will be found in an illustration given by Elwes (1913) and reproduced by Wallace (1923). It is probable that the amount and nature of the spotting is readily amenable to selection and the varying appearance of different flocks is due to the type of pattern that has been chosen as the ideal.

Piebald sheep breed remarkably true, the writer having quite failed to discover any instance of a lamb other than Piebald being born in a Piebald flock. One breeder writes "...The farm steward tells me that he has *never* seen one of these sheep wholly black or wholly white." This reply is typical. Such observations as the writer has been able to make appeared to show that the correlation between the type of spotting in mother and offspring is not very high.

The black patches in new-born lambs are as dark as the black exhibited by other black sheep, but as the lamb grows the colour becomes transformed into a brown or even a fawn, this change being much more marked than the usual bleaching seen in ordinary black sheep.

It might be mentioned that while the sheep in the majority of flocks are four-horned a number of flocks are in existence which consist solely of two-horned sheep, so that this feature cannot be regarded as a breed characteristic, and may possibly have even been introduced by crosses with other primitive four-horned breeds. There is no doubt, however, that certain flocks have been four-horned for a very long period.

2. *Crosses with Other Breeds. The* F_1 *Generation.*

It has been frequently recorded that the result of crosses with other breeds is the production of self-blacks only, and that many of the F_1's exhibit "white pattern" which consists of a white spot on the top of the head and a white tip to the tail. Noble (1913) states: "Now it is a curious fact that when our piebald sheep are crossed with any other domestic breeds, the lambs are practically all born black with a white patch on the forehead and partly white tails." Elwes (1913) quotes this statement and mentions the fact that he crossed piebald rams to ewes of many breeds apparently with the same result. Portal (1923) states that self-blacks result from crosses with Highland sheep, Border Leicester, Southdown, and Cheviot sheep. He also states that two lambs from a wild Moufflon ram and a Piebald ewe were self-blacks with white pattern. Mr R. Holland Martin, of Overbury Court, Tewkesbury, informs me that his Piebald sheep have been crossed with Oxford Downs in previous years with the same result.

In the autumn of 1923, Major E. J. W. Platt, of Gorddinog, Llanfairfechan, wishing to test this statement, made reciprocal crosses between Piebald sheep on the one hand, and Southdown and Welsh Mountain sheep on the other. The writer had the opportunity of examining the lambs: all were black, though in the case of the Welsh crosses one or two showed very extensive white pattern. These lambs possessed several little white tufts especially about the shoulders. It is probable that the white tufts would only exist in the lamb's coat. The writer also had the opportunity of seeing some Piebald-Kerryhill F_1's born in the flock of Sir Gerald Corbett, Bart., Acton Reynauld, Shrewsbury. Fifty of these lambs were raised, and all were black; in six cases only was the white pattern so extensive as to be specially noted.

To the general rule that the F_1's of any cross are self-black, the writer knows of two exceptions. The first is recorded by Elwes (1913) who mentions one particular Piebald ram which when mated to Fat-rumped ewes gave four blacks and one white. The same ram mated to a Wiltshire × Soay ewe gave one piebald lamb and one white. The other case came under the writer's personal observation. Major Platt in 1924 crossed a Dorset Horn ram to two Piebald ewes, the result being four piebald lambs. The same ram mated to another ewe in 1925 sired two more lambs, both piebald. These lambs are shown in Plate XI, figs. 8–11. It will be seen that though some are perhaps not typical, they fall within the limits of variation of the pattern.

One additional point is worthy of mention. It has been noted above

that it is characteristic that the black colour of the pigmented patches in the pure breed becomes transformed into a brown or fawn. This does not appear to be the case in the black coat of the F_1's. It has only been possible to examine two F_1 sheep that have attained the age of a year, and both possessed coats at that time that were no lighter than those usually seen in black sheep.

3. *Further Experimental Breeding.*

To obtain further information as to the inheritance of the piebald pattern, F_1 rams were back-crossed to white and to piebald sheep respectively. In the first case a Piebald-Southdown F_1 ram was crossed to white Welsh Mountain ewes, this experiment being carried out by Major Platt. In the second case a Piebald-Black Welsh Mountain F_1 ram[1] was crossed to Piebald ewes, this experiment being carried out at the farm of the University College of North Wales, Bangor.

The results were as follows:

TABLE I.

Self-black F_1 ♂ × White ♀.

Ewe	Sex of lamb	Phenotype of lamb	White pattern
1	♂	White	—
1	♀	White	—
2	♂	Black	None
3	♀	Black	White tuft on head only
4	♂	White	—
5	♂	White	—
5	♂	Black	White tuft on head only
6	♀	Black	White tuft on head only
6	♀	White	—
7	♀	Black	White tuft on head only
7	♀	White	—

TABLE II.

Self-black F_1 ♂ × Piebald ♀.

Ewe	Sex of lamb	Phenotype of lamb	White pattern
S 37	♂	Piebald	—
S 38	♀	Black	Head only
S 39	♂	Black	Head only
S 39	♀	Piebald	—
S 40	♀	Black	Head only
S 40	♀	Black	Head only
S 41	♀	Piebald	—
S 41	♂	Piebald	—
S 42	♂	Piebald	—
S 42	♀	Piebald	—

[1] The choice of a Black Welsh × Piebald ram for the second back-cross rather than a Piebald × white ram was due to the fact that this ram was also being crossed to white ewes to test whether the dominant black of the two breeds depends on the same factor, and in this way it was possible to economise space at tupping time by using the one ram for the two purposes.

In the case of the back-cross to white, segregation was perfect. The white pattern exhibited by the blacks was not extensive and did not involve the tail in any case (Plate XI, figs. 6–7). The F_1 ram used in the cross did not exhibit the pattern at all. The four blacks resulting from the back-cross to piebald were ordinary blacks, but in this case the white pattern was more extensive (Plate X, fig. 5). It still did not involve the tail. Five of the six piebalds were well within the normal limits of the spotting, but one lamb was extremely dark, the white areas being reduced to a more or less white face and a few extremely small white areas on the body, which, however, involved more than the lamb's coat, so that there is little doubt that this lamb was genetically piebald and not black. The F_1 ram in this case had also exhibited fairly extensive white pattern on the head, the white patch including a small area of the stiff hairs of the face, so that this small area of white was persistent.

4. *Discussion.*

The numbers involved in the experiment are small, but it may be stated with considerable confidence that Piebald sheep differ from ordinary white sheep in that they possess a dominant black factor and a recessive pattern factor. The back-cross ratios, six whites to five blacks in the back-cross to white, and six piebalds to four blacks in the back-cross to piebald, are sufficiently good evidence of this. The two cases quoted above where Piebald F_1's appeared, are to be explained on the assumption that the white parent in each case possessed the pattern factor. This is confirmed by an experiment mentioned by Ewart (1919) where some of the F_2 sheep of a Southdown × Soay cross were piebald. It is significant that in the case of Elwes' piebald F_1, the mother was a crossbred Soay. The experiments alone do not directly answer the question as to whether a white sheep homozygous for the pattern factor would still be white, but this is very probable. The Dorset Horn ram which sired six piebalds would most probably be homozygous for the pattern factor, and the fact that piebalds do not occur in ordinary white flocks strengthens this argument. It may be accepted then as reasonably certain that the piebald pattern factor only produces an effect on a sheep that is already pigmented. It is probable that the extreme range of variation in the extent and nature of the spotting is to be ascribed to a number of modifying factors and that a certain amount of variation may be non-genetic (Sewall Wright).

The constancy with which piebald lambs only are produced in Piebald flocks indicates a high degree of genetic purity which is inevitable in the

case of the recessive pattern factor but not so in the case of the black factor. The case of Elwes' ram which sired two white lambs is to be explained on the assumption that he was heterozygous for the black factor.

The two Piebald-Dorset Horn F_1 lambs born in 1926 exhibited almost precisely similar markings (Plate XI, figs. 10–11). These markings, as far as the ventral surface is concerned, are not unlike those described by the writer and Jenkin (1926) and termed "reversed badgerface" pattern. The writer's opinion is that this resemblance is accidental or might be the expression of a general tendency to exhibit a light-coloured belly, and this opinion is strengthened by the fact that the four lambs sired by the same ram and born in 1925 were in no special way remarkable as regards their spotting.

White pattern is of interest because of its universal distribution in the case of coloured sheep. It is most fully dealt with by Adametz (1917) who considers that it depends upon a single recessive factor together with another main modifying factor (see also Elwes, 1912, 1913; Wallace, 1915; and Roberts, 1924). The only special point in the present work is the frequency with which the head and tail markings are not associated.

It is hoped to deal with the question of the relation of the dominant black of the Piebald breed to that of the Black Welsh breed at another time, and it is also hoped that data will then be presented which will indicate whether the bleaching of the black wool of the Piebald sheep is capable of a simple genetic explanation.

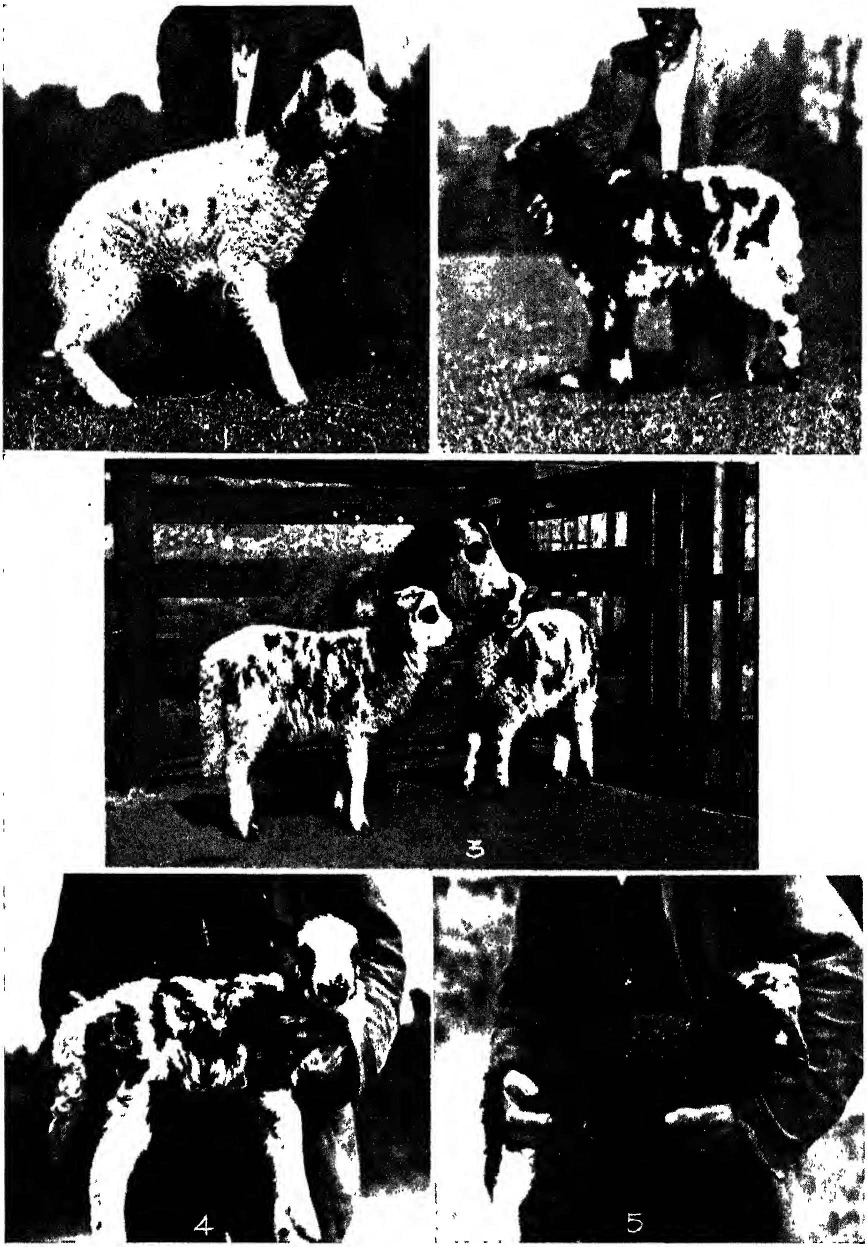
The writer wishes to acknowledge the help received at all times from Prof. R. G. White, of the University College of North Wales. He is also indebted to Major Platt and to Major Platt's farm manager, Mr Coward, for the facilities for observation placed at his disposal, for the information they have supplied and for so readily consenting to carry the experiment further. The writer is indebted to Mr Holland Martin and to Mr Hall, of College Hill, Shrewsbury, for much useful information.

5. Summary.

1. A brief description is given of the Piebald breed of sheep. While there is a considerable range of variation in the extent and nature of the spotting these sheep breed remarkably true for the piebald character.

2. The result of crosses with other breeds is the production of self-blacks.

3. A back-cross of the F_1 to white gave six whites and five blacks. A back-cross of the F_1 to piebald gave six piebalds and four blacks.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3
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4. Piebald sheep differ from other breeds in that they possess a dominant black factor and a recessive pattern factor which restricts the black to certain areas.

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DESCRIPTION OF PLATES X AND XI.

PLATE X.

Fig. 1. Lightest Piebald lamb in Major Platt's flock, 1926.
Fig. 2. Darkest Piebald lamb in Major Platt's flock, 1926.
Fig. 3. Piebald ewe with lambs showing medium spotting.
Fig. 4. Back-cross. Black F_1 × Piebald—piebald lamb.
Fig. 5. Back-cross. Black F_1 × Piebald—black lamb. Extensive white pattern on head.

PLATE XI.

Fig. 6. Welsh Mountain ewe with lambs from Piebald-Southdown F_1 ram.
Fig. 7. Black lamb (Black F_1 × white back-cross) showing restricted white pattern on head.
Figs. 8–9. Piebald ewes with four piebald F_1 lambs sired by Dorset Horn ram, 1925.
Figs. 10–11. F_1 piebald lamb sired by same Dorset Horn ram, 1926.

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PHYLOGENY AND THE NATURAL SYSTEM.

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CONTENTS.

I. INTRODUCTION.

THE general acceptance amongst biologists that species of animals and plants are related to one another by descent was followed by numerous endeavours to revise the system of classification, and to place it on a basis of genetic relationship. To-day these endeavours to construct a natural system have been to a large extent abandoned. The efforts, which involved an extensive investigation into all kinds of structural characters throughout the families of organisms, both living and fossil, and had for their object the arrangement of each genus, and even species, in its correct systematic position, have apparently failed to attain that degree of success which has attended other lines of biological investigation. Within recent years, experimental biology has proliferated to such an extent that it now possesses numerous special periodicals; even the endocrine secretions are not without their own peculiar journal. Great success has attended the culture of bacteria under totally unnatural conditions, and cultural methods have recently been applied to isolated portions of animal tissue. No less remarkable have been the results obtained from artificial fertilisation and the development of the egg in an artificial environment. In genetics, T. H. Morgan (87) remarks on the fact that "the fundamental aspect of heredity

should have turned out so extraordinarily simple," and he has not only located the factors of heredity on the chromosomes but in one case has told us how these genes are arranged. On the other hand, current zoological and botanical literature reflects a loss of interest in phylogenetic research which contrasts strongly with that seen during the immediate post-Darwinian period, but which is obviously not due to the attainment of a fixed scheme of classification. In no group of animals or plants has any particular system been proved definitely superior to all others. At present, in fact, the efforts of taxonomic and phylogenetic work of the end of the last century are looked upon, in some quarters, as misdirected in aim, however valuable the results incidentally obtained may be.

This state of affairs appears to be the outcome of at least two different trends of investigation. On the one hand, systematists themselves, finding the results of their detailed studies impossible to frame in a simple phylogenetic series, have frequently condensed their results in such a manner that obvious anatomical facts were overlooked, and fantastic interpretations placed on structure, in order to bring the facts into line with a preconceived simple scheme. Instances of this are met with in the history of the classification of nearly every group. Even to-day some phylogenetic problems remain in this state. It is possible to compare the Vertebrate type, for example, with that of almost any group of Invertebrates by making the necessary preliminary assumptions. All hypotheses, including those incidental to phyletic speculations, are of course representations of the facts, not the facts themselves. In many of the phyletic hypotheses that have been put forward in the history of the subject the representation has however been made in such a manner that subsequent observers, by the accumulation of additional facts, have been able to show the inadequacy, or at least the disadvantages of these phyletic speculations, and consequently the artificiality of the systems of classification based on them.

On the other hand, the possibility of formulating a natural system has been challenged by the introduction of Mendelian ideas into heredity. In the course of evolution a number of inherited variations must have come about and have given rise to the different types characterising the various species, genera, families, orders and classes. The variations observed in Mendelian experiments are inherited, and of late years have been considered as, in part at least, identical with those responsible for the origin of species. No one will doubt that there is some degree of analogy. Mendel's crosses were made between forms differing only in

characters that are regarded as of sub-specific (varietal) rank. But in many subsequent experiments species have been crossed and the offspring proved fertile, the specific characters behaving in a Mendelian manner. Attempts have therefore been made to explain species differences on a chromosome basis. The bearing of these Mendelian theories of evolution on the question of phylogeny will be discussed in the following pages. It is sufficient here to point out that the criticism by the Mendelian theorists of the older phyletic theorists rests on the assumption that a knowledge of the method of evolution is necessary for the construction of a phylogenetic hypothesis. They agree that if Darwin's view, that gradual variations were chiefly responsible for evolution, was the last word on the subject, then the reconstruction of phylogenesis would be possible, but they think they have discovered some new facts regarding the nature of the variations responsible for evolution, and that these facts make phyletic reconstruction impossible.

The object of the present work is to put forward some considerations which have been arrived at by the author during some ten years of study of specific differences in simpler types of organisms, and their bearing on phylogeny in general. A consistent account of phylogeny does not appear to have been given since the subject was first defined and investigated by Haeckel (49, 52). This author, and the earlier workers in general, especially Hyatt (63) and Cope (19), had clear ideas on the subject, although their terminology was a complicated one. But these earlier concepts must now be looked at from a different point of view. It would be out of place here to recapitulate all the older arguments for, and give examples of, phylogenetic hypotheses. There seem, however, to be certain points of view which have hitherto remained obscure and have been overlooked both by antagonists of phylogeny and by the phylogenetic speculator. It is impossible to present these clearly without brief reference to historical matter, as questions of scientific method are involved, and also without giving a short résumé of the well-known principles on which phylogeny is constructed.

II. Development and Classification.

What are the limits of phylogeny, and what are its relations with botany and zoology? The term biology was used as early as 1802 by Treviranus (111) to indicate the science of living organisms in general. Although the word has been much used on the Continent in a narrower sense the wider meaning is now being accepted again, and is practically universal in this country. Biology is commonly divided, then, for

practical purposes into botany and zoology, but a more philosophical method of division, and one which appeals to those interested in organisms in general, is derived from the fact that both animals and plants can be studied in at least two different aspects. It is thus the distinction between physiology and morphology comes about. As many authors have pointed out, the physiological and morphological points of view are not mutually exclusive, rather they should be considered as supplementary. A recent notable contribution on this subject is that of E. S. Russell (98). Nevertheless the physiologist is constantly making use of the concepts of physics and chemistry in explaining the life processes, whereas the morphologist considers every form in terms of evolution.

Owing to the failure of morphologists to be interested in energy changes as understood by the physicist and chemist, some recent writers have considered morphology as confined to the statical aspects of life alone. P. Geddes and J. A. Thomson, in their introduction to biology (43), include all dynamic aspects of biology within physiology, and thus phylogeny, as the science of race development, falls under the latter in the scheme of the biological sciences given by these authors. Again, A. G. Tansley (108) thinks the separation of morphology and physiology ultimately depends on two distinct types of human mind, the one attracted by objects, the other by processes. Nevertheless he still appears to relegate phylogeny to the morphological sciences. As a matter of fact the view of morphology as confined to, or even chiefly concerned with, the static aspects of organisms is incompatible with the history of biology and of the leading concepts of morphology. It is doubtful whether the idea of a general science of form would have existed if the dynamic concept of "metamorphosis" had been unknown to its originator (47). For the principles and even the name of the subject can be traced to Goethe (48), who defined morphology as the attempt to understand the relationships of the "external visible parts" of organisms. It is therefore quite unnecessary to speak of "comparative" morphology, since the word by definition includes this. Another misconception is that of Goebel (46), who is under the impression that the internal anatomy is excluded by Goethe's reference to external form. But the latter includes all the tangible features of organic bodies, and was contrasted by Goethe with inner activity as an intangible force working on the material of the organism in the same way that the mind of an artist becomes manifested in his work[1]. Goethe's metamorphosis was undoubtedly an evolutionary concept, but much vaguer of course than

[1] See E. S. Russell (98) for a concise account of Goethe's views.

that of post-Darwinian authors. The recognition of relationship by descent made morphology an exact science, but its comparative methods remained in essence unaltered. The dynamic nature of the subject was clearly expressed by Darwin (29), who also says of it, "This is one of the most interesting departments of natural history, and may almost be said to be its very soul." Haeckel (49) gave a full account of the scope of morphology, enunciating the principles laid down by Goethe in remarkable clear form, made possible by the acceptance of evolution in its definite modern significance. But even before the appearance of Darwin's great work, morphological concepts had made their appearance in botany, owing to the work of A. de St Hilaire (100) and had been introduced into zoology by H. D. de Blainville (8), who first employed the word "type" in its morphological significance. To Goethe's conceptions E. G. de St Hilaire (101) added the "principle of connections," viz. that similar parts occupy similar relative positions in all animals.

Correspondence of form then, leading to dynamic views of transformation, was clearly recognised before relationship by descent was accepted. It appears at this stage of the history of the subject to be something more than the mere comparison of the forms of organisms, the latter type of comparative anatomy being traceable as far back as Aristotle or even earlier (98). Goethe had already detected, although vaguely, a process by which organisms were related and had called it "metamorphosis" (47). He even gave to this process a sense of direction as shown by his distinction of ascending and descending metamorphosis and of expansion and contraction of organs. A. de St Hilaire went still further than this and distinguished various methods by which changes of structure come about. Later authors, having obtained clearer ideas on evolution, were able to deal with this part of the subject in greater detail. It is unnecessary to describe the classification of the changes assumed to take place in evolution here, however, since the conclusions that these different processes have taken place are all arrived at by precisely the same method, namely, by comparing numerous species one with another. And in later morphology the comparison has embraced the embryonic characters of the species concerned, whilst such characters as have persisted from fossil species have also been included.

From a study of the adult organism of a given species, especially if it had a complicated structure as in Man, many facts regarding the development of that species might be inferred. Fortunately embryology has a more direct method of study, namely, by observation of the actual stages of development. This information is necessary for a complete

description of any one species, since the anatomy of any one stage differs from that of another, the whole series constituting the ontogenesis or life cycle of the species. Thus besides anatomy, which itself has a dynamic aspect owing to the possibility of comparing the different parts of the adult organism with one another, morphology must include ontogeny, the science of individual development, embracing all those changes which occur between fertilisation and death, not only the development of the embryo in its narrow sense (Embryology) but all processes of metamorphosis and even changes taking place in old age.

That physiology, as ordinarily understood, cannot affect the findings of phylogeny[1] is indicated by the following considerations. The aim of physiology is to form a complete physico-chemical conception of the organism as far as is possible. It therefore analyses the activities theoretically, including the development of the race, into the activities of atoms and molecules. The aim of phylogeny is to reconstruct the history of the race in the same way as the embryologist reconstructs the history of the individual. The units of embryology are cells, organs and various segments of the body of other kinds. An exact account of the development of the individual can be given in the terms of these concepts, and such an account is independent of the physico-chemical processes underlying these morphological units. The same applies to the history of the race; it must be visualised in morphological units, many of which will be comparable with those used in individual development, although not necessarily identical, because the units must be capable of existence in adult organisms.

Apparently the word phylogeny was first employed by Haeckel (49) and defined by him as "the science of the form-changes which the phyla or organic races pass through during the whole period of their individual existence." It is thus a branch of morphology bearing the same relation to taxonomy as embryology does to anatomy. The process of race development itself was later (52) termed phylogenesis by Haeckel, who adds the following: "The science which has for its object the empirical knowledge of these historical facts, and the philosophical perception of their causes, we call race-history or *phylogeny*. From the nature of the facts the latter belongs to the *historical* natural sciences, for it investigates events the direct observation of which is, in by far the greater part, impossible." He then says that this does not prevent it from being an exact science. By assigning to phylogenesis a causal rôle in ontogenesis,

[1] Evidence from serology strongly confirms morphological conclusions, but only the latter will be discussed here.

Haeckel introduces the factor of heredity into the arrangement of the whole life cycle and from this point of view, although his explanation is in no way a remarkable one, it would appear as something more than "mere rhetoric" as E. S. Russell (98) calls it.

The introduction of genetic ideas into classification in the first instance was due to Darwin (29), who however made no attempt to apply his principles in detail. Haeckel not only enunciated clearly nearly all the assumptions upon which morphologists, including taxonomists, are still working (49); but he also made an attempt to trace in some detail the lines of evolution of all the groups of organisms (50, 52). A very large number of terms in common use in biology are also traceable to this author. Yet perhaps no other writer on biological subjects has been so misrepresented[1]. His ideas and observations are seldom considered in relation to the state of biology at the time. Possibly his contributions to general biology would have received greater recognition had he not also presented them in popular speculative works (53, 54) combined with a vigorous attack on the Christian Churches.

Haeckel (52) considered that part of phylogeny was concerned with causes of phylogenesis. In another place (51) he says that phylogeny is the cause of ontogeny; it is therefore clear that he considered an evolutionary explanation possible, as well as a physico-chemical one. Modern causal morphology (68, 109) appears to recognise only the latter kind of explanation, but in so doing it excludes the action of heredity for which at present we have no satisfactory physico-chemical explanation, although several ingenious attempts to deal with the problem from this point of view have been made (30). Haeckel's views therefore are more satisfactory than some modern ones, like those of W. H. Lang (68) and D'Arcy Thompson (109), not because they were more precise, but because they recognised the immense importance of the inherited factor.

The natural system is an older concept than that of descent. To define the natural system in its present form in a manner which will not do violence to its historical associations means that it must be considered as an arrangement of species in genera, families and so on, in such a manner that the members of a given genus are more closely related to one another by descent than are the members of different genera, whilst

[1] An example of this is even to be found in a recent work (93) of E. Perrier, who represents Haeckel as continuing to insist on the existence of *Bathybius* as a real organism in spite of the fact that Huxley, its discoverer, had recognised it to be of artificial and mineral origin. Haeckel clearly abandoned *Bathybius* in his later works, as also many of his *Monera*.

the same applies to the groups of higher order, such as the family, order, class and phylum, in which however the relationship becomes increasingly less. All known species, whether living or extinct, may be included in the natural system; this is not however synonymous with phylogenesis, which differs for each species and consists of a series of ancestral forms, many of which are hypothetical. The system is arrived at by comparing organisms with one another; and is a perfectly definite arrangement capable of being expressed in exact terms, although of course more difficult to describe than a physical structure. The statement that one leaf is just twice as long as another is quite as definite a statement as that one leaf is three inches long. The difficulty rests in the fact that in the first case we are describing one organism in terms of another, whereas in the latter case we describe it in terms of an artificial standard. A natural system is a real system of relationships, and not a mere arbitrary arrangement, although it is not of course and perhaps never will be possible to give a detailed account of it as a whole.

III. The Construction of a Phylogenetic Series.

It is commonly supposed that the unicellular stage preceded the multicellular in the course of evolution. The Protozoa would thus represent an ancestral group from which the Metazoa have been derived. But even this has been questioned. Dobell, for instance, sees (34) no reason for regarding the Protozoa as more primitive than the Metazoa, basing his view on the supposed non-equivalence of the individual cells of Protozoa with the tissue cells of Metazoa. Several reasons for not accepting this extreme point of view will appear in the subsequent paragraphs; here we may merely refer to the fact that the gametes of the higher animals, and the gametes and spores of tissue-forming plants are undoubtedly homologous with tissue cells, as is shown by their origin, and yet gametes in some cases differ less in structural characters from protozoal cells than many of the latter do amongst the different species of Protozoa. The ovum of *Hydra* for instance more closely resembles the active stage of an *Amoeba* than the latter resembles many other Protozoa. The gametes of many Algae, even when differentiated into male and female, are often almost indistinguishable from Phyto-flagellates. The sperms of animals are usually highly modified but are not without resemblance to Protozoa; in *Triton* for instance the tail is furnished with an undulatory membrane not unlike that of the trypano-somes. Especially is there a resemblance between Protista and the spores

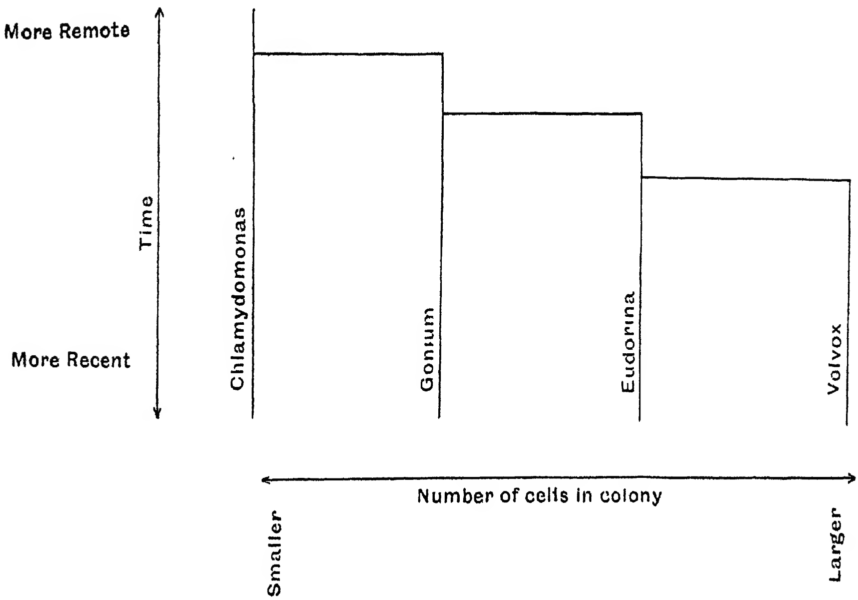
of plants, definite unicells which show homology, as evinced by development and structure, with the tissue cells of Cormophyta on the one hand and with the resting stages of unicellular Algae on the other.

The majority of authors never question the supposition that multicellular animals and plants have arisen from unicellular ones and, as far as the primitive multicellular types are concerned, the simplest view, and the one most commonly accepted, is that they arose gradually from larger and larger colonies of protozoan or protophytic cells. The problem as to whether the Protozoa are more primitive than the Metazoa is one of the greatest that the morphologist has to solve and is, further, absolutely typical of phylogenetic problems. The method which is adopted in any attempt to solve this problem can be used equally well to attack thousands of other exactly comparable although often less difficult phylogenetic problems. In each case we must begin with living organisms of well-known structure and life history. Since the general question of the origin of the multicellular from the unicellular state is to be considered, a large number of possibilities exist. Each of these possibilities may have at some time been realised in the natural system, but it will be sufficient here to consider, as an illustration, one natural series which will be seen in some respects to represent phylogenesis. No attempt will be made to prove that the larger Metazoa arose from the Protozoa by the colonial method, but rather that a passage from unicellular forms to colonial forms in phylogenesis has taken place in at least one instance.

Species or genera of a given systematic group can frequently be arranged in a series, according to the degree of development of one particular character, common to the members of a group. One of the best-known instances of this is to be found in a series of genera of phytoflagellates, including the well-known *Volvox*. The latter represents the largest and most complicated of a series of forms which can be arranged in order of size and complexity of their colonies. The smallest and least complicated is *Gonium*, a genus which includes both 4- and 16-celled species or forms, and thus closely approaches the unicellular state which is represented in the series by *Chlamydomonas* and allied genera, which resemble *Gonium* in characters other than colony aggregation.

It is usually supposed that the above-mentioned genera represent a phylogenetic series. In other words that *Volvox*, in the course of its evolution, has descended from extremely remote ancestors belonging to the other genera. Thus *Chlamydomonas* appears as an older genus than

Gonium, the latter than *Eudorina*, and this in its turn than *Volvox*. This may be expressed graphically thus:



Number of cells in colony is naturally closely correlated with size of colony, but it is also correlated with other variations in character which are not mere mechanical effects of number of cells. Thus both *Eudorina* and *Volvox* show a differentiation of male and female gametes, and this heterogamy is more pronounced in the latter genus than in the former. *Gonium* is isogamous, as are most, although not all, species of *Chlamydomonas*. A further feature of the series is that reproduction is confined in *Volvox* to a minority of cells of the colony, whilst in the other genera mentioned reproduction is universal.

Hence it is not only possible to arrange the four genera in a series on the basis of number of cells in the colony or size of colony, but also, if the genera are arranged in the particular sequence resulting from a consideration of this character they are also to some extent arranged in the sequence which would result from a consideration of the sex differentiation or the extent of the reproductive area of the colony.

Further facts suggest that such an arrangement is not arbitrary but expressive of some natural seriation. For besides the genera mentioned there are several allied ones which could be considered. *Pandorina* is a

monotypic genus of similar cell structure to *Gonium* and *Chlamydomonas*, but in which the colonies are generally 16-celled, *i.e.* as many as in the largest colonies of *Gonium*, but may contain 32 cells as in *Eudorina*. The colonies are larger than those of *Gonium*, if account is taken of the difference in shape, but are considerably smaller than those of *Eudorina* which they resemble in form. The gametes show indications of heterogamy by a slight difference in size and degree of motility; in the sex character *Pandorina* is thus intermediate between *Gonium* and *Eudorina*. The colonies normally reproduce by division of each cell of the colony.

Another genus or generic form belonging to the same family is *Pleodorina* consisting of two known species or forms. The number of cells in the colony is intermediate between that of *Eudorina* and *Volvox*. Not only so but the area of reproductive cells attains the degree of development that would be expected from its intermediate size, and of the two species the smaller has the larger reproductive area, almost approaching the condition seen in *Eudorina*.

The arrangement of these colonial Chlamydomonads, which is suggested by the characters of colony size, sex differentiation and degree of some development, is roughly a linear series. The correctness of the linear arrangement[1] is however supported by independent evidence from the development of the colonies. The colonies of *Gonium* have the form of a disc throughout their life, but in the other genera the adult colony has the form of a hollow sphere or ellipsoid. Nevertheless in all these forms the young colony has a discoid form and it is by invagination of this disc that the adult form is arrived at.

It is scarcely necessary to dwell on the facts, as comparable examples are well known to systematic morphologists in practically every group of animals and plants. It may be regarded as definitely established in a large number of cases that:

(i) if a number of species may be arranged in a series in respect to the degree of development of one character they are also *ipso facto* arranged in a series in respect to other characters, (ii) characters that may be used to give such a seriation include characters of the juvenile, as well as of the adult phase.

In the series referred to, as in other series of an approximately linear kind, the terminal members are distinguished on the one hand by their relative simplicity and on the other by their relative complexity. Not only are the colonies of *Volvox* built up of a much larger number of

[1] A criticism of the linear arrangement is made later.

cells than those of *Gonium* but also there are measurable differences between the individual cells, so that vegetative cells and asexual reproductive cells, as well as distinct male and female gametes, can be distinguished in the different colonies in *Volvox*, whereas in *Gonium* all cells appear to be of one kind. Further, not only is there greater spatial differentiation, as this variation in the cells of the colony may be called, but there is also greater temporal differentiation in the life cycle, for *Volvox*, as distinct from *Gonium*, shows a marked difference in form between the various stages of colony development.

The fact that series exist in the natural system, and that these series show progressive differentiation, was known before evolution was accepted as an interpretation. Without assuming that the series we have discussed is necessarily a representation of phylogenesis let us see whether there is any evidence that implies a direction. It is generally assumed that the simpler forms preceded the more complicated. What facts can be derived from comparative morphology indicating that progression has taken place in one direction rather than in another?

An answer to this question is easily found by examining a large number of genera which have characters similar to those seen throughout the colonial Chlamydomonads, viz. biflagellate cells, green chloroplasts, pyrenoids, starch, eye-spot, contractile vacuoles. It is found that there are a number of other genera possessing a combination of these characters, but none of these other genera have the colony form of *Volvox*; they are practically all unicellular and many closely approach the structure of *Chlamydomonas*. These unicellular *Chlamydomonadaceae* afford a connecting link, as far as their actual structure is concerned, with a large number of other Flagellates and Algae, and hence with the rest of the animal and vegetable kingdoms. Thus the series of colonial Chlamydomonads has a direction in the sense that, in respect of certain actual characters, some members more closely resemble the rest of the animal and vegetable kingdoms than do the others. In this sense *Gonium* is the first of the series, because it most closely approaches the typical forms of plants and animals, and *Volvox* is last because it is the most aberrant.

These facts, which have been recognised more or less clearly by systematists for a considerable time, have been expressed as a phylogenetic series. It is said that a diagram, such as the following, which agrees with that given by F. F. Blackman (6) and Cavers (17), but omits doubtful forms, represents the phylogeny of the group.

Volvox
↑
Pleodorina californica
↑
Pleodorina illinoisensis
↑
Eudorina
↑
Pandorina
↑
Gonium
↑
Chlamydomonas

Many similar series of forms are known from the most diverse groups of the animal and vegetable kingdoms. All the conclusions of phylogeny are based on the existence of such series. In Algae we could for instance trace a series from unicellular form to colonies, and from simple filaments through branched filaments to massive thalli. In Bryophytes excellent examples of linear series are met with in the comparative morphology of the sporogonium resulting from progressive sterilisation of the sporogenous tissue. Bower (13) even attempted to trace a gradation of the same kind throughout the sporophyte of the Cormophyta. The seriation of sporophytes with respect to the restriction of the sporogenous area of the plant may be cited as an undoubted example of series in the natural system. Flowers themselves show numerous series. In segmented Invertebrates excellent examples of series beginning with species with undifferentiated, numerous segments and concluding with those in which the animal is compacted of differentiated segments, limited in number, are found. The Crustacea offer a good example. The gametophyte of Bryophytes shows a similar progressive differentiation, but in the Vascular Plants the gametophyte has a reverse seriation to the sporophyte. Vertebrates give similar series; the system of the teeth may be given as affording many excellent series. But very many other examples are known and for a concise account of these, especially in some of the smaller groups, reference may be made to the work of Cope (19).

The whole of plant and animal morphology in fact bears witness to the same kind of thing. The instances given are only striking because the series are comparatively long and fairly simple. Usually complex branched systems of relationships result when even a comparatively small number of characters in a small number of species are considered. The existence of series is an essential part of the evidence for evolution. But evolution cannot be confined to some species alone, and if the systematic arrangement has any phylogenetic significance in the one case it must also have a similar meaning in the other. The question of

branched representations of relationships will be dealt with later; at present an attempt must be made to decide whether the above diagram represents the course of phylogenesis of the genera named in it, and if so in what way.

In the colonial Chlamydomonads the members of a series in the diagram are all living forms, and owing to the soft character of their bodies no trace of fossil remains of their former representatives are known. But exactly similar phylogenetic series can be constructed in groups containing a number of fossil members. Reference has already been made to the systematic differences in the teeth of Vertebrates as sometimes forming series. The Elephants differ from other *Ungulata* in various anatomical characters, but particularly in the large size of their body, and the specialisation of the head. One feature is the enormous enlargement of the incisor teeth of the upper jaw to form tusks, accompanied by reduction in number of the other teeth. Several fossil genera are known. Of these *Moeritherium* has the second pair of incisor teeth in each jaw enlarged to form small tusks. *Palaeomastodon* has the upper tusks larger, *Tetrabelodon* still larger, but still curved downwards or straight, and finally comes *Elephas* with its upwardly curved incisors now forming typical tusks. Thus, as far as one character is concerned, namely that of the upper jaw incisors, the four genera mentioned form a series leading back to the more typical *Ungulata*. It so happens that the same arrangement is borne out by a number of other characters, but not by all. The question of the selection of taxonomic characters will be discussed in a later chapter. Here it may merely be stated that the arrangement of the genera given above, and based on a number of characters, coincides with the arrangement of the fossil remains of these genera in the various geological formations. *Moeritherium* is found in the Middle and Upper Eocene, *Palaeomastodon* in the Upper Eocene, and may extend into the Oligocene, *Tetrabelodon* belongs to the Miocene and Lower Pliocene, *Elephas* appears in the Upper Pliocene, Pleistocene and Recent deposits.

The phylogeny of the genera of the Horse family *Equidae* presents exactly analogous features. This is usually regarded as a case of regressive evolution, the whole series being looked at from the point of view of reduction in the number of the digits. The question of regression will be discussed later. But it may be pointed out that the progressive enlargement of the middle digit is accompanied by increase in body size, changes in the head and neck and dentition, thus perfecting the grazing mechanism (31), whilst the numerical reduction of the other digits with

enlargement of the middle one may be compared with the reduction of molars with enlargement of the incisors in Elephants.

It so happens that, in by far the majority of groups containing fossil members where phylogenetic series have been traced, the order of the members, as arrived at by comparative anatomical investigations, coincides with their arrangement in the geological strata; further, the oldest fossil members are the more generalised forms and serve to connect the recent species with the rest of the animal or vegetable kingdom. Thus in the Horse series the oldest members are small five-toed types and are in every respect more typical mammals than are the members of the genus *Equus* itself. The palaeontological aspects of phylogeny have been discussed very fully in many of the works of the earlier authors, especially Hyatt (63) and Cope (19), and also in a number of recent ones, of which the monograph on phylogenesis by Dürken and Salfeld (37) may be mentioned. It is a mistake to suppose however, as the latter seem to suggest, that palaeontology supplies the true phyletic series. For a mere sequence in the strata of successive geological periods does not indicate relationship. In fact relationship of fossil organisms to one another must first be traced in exactly the same manner as that of living forms, and any arguments as to their relationships based on their stratigraphical arrangement are entirely secondary. They may confirm the morphological data, but can never replace them. It is possible too that a living form may more closely represent the ancestral form of another living species, or even of a fossil form, than any fossil species yet discovered.

To apply the axiom of individual heredity, that like tends to produce like, to species as well as individuals, is hardly an assumption. A new species will differ from its progenitors, but its differences will be extremely small as compared with its resemblances. The whole of evolution rests on this assumption. Even extreme mutationists will admit this. And mutationist ideas in extreme form are rare at the present day. E. Geoffrey de St Hilaire (101), although an evolutionist, believed that "a crocodile's egg could grow into a bird," but few modern authors will be found to agree with him. Some arguments for occasional mutations of an extreme type have been given by Bonavia (see 42), but on the whole, mutation, as accepted by modern investigators, means very small change from the point of view of the taxonomist.

Unless one believes in a view that practically amounts to special creation, it will be admitted that species closely related by descent, whether linear or collateral, are similar. Suppose a group of living

species to be descended from a common ancestral species. Then the average characters of this group are the ones which most nearly approach those of the common ancestral species. But even the average members of the group may have diverged from the ancestor. Nevertheless it must be assumed that the average species are closer reproductions of the ancestral type than are the extreme species. And it is extremely unlikely that they will all diverge from the ancestral species to the same extent. We know that in the genealogy of individuals this is not so; and if there is one point upon which palaeontological evidence is definite it is that species and other groups have changed to a very varying extent in the course of the earth's history. While some species, or at least genera, have remained unchanged, classes and even phyla have been evolved. The genus *Lingula*, for example, has been traced back to Cambrian formations.

If the whole natural system or any part of it be considered, the various constituent species are found to have certain features in common, although the larger the group taken the fewer will be the common characters. Yet even throughout the natural system as a whole there are certain common features. A morphological character common to almost all animals and plants is, of course, that of cellular structure. Now if there is an inherited resemblance between related species, as there is between individuals, then the characters that are common to a group must also have been present in the immediate common ancestors of that group. Hence in the *Volvox* series the cell characters, such as the presence of two flagella, a single green chromatophore, an eye-spot and so on, which are constant throughout the group, are ancestral. Now *Chlamydomonas* is a genus which has little but cell characters; there certainly is never any colony of the coenobium type. Hence one might expect *Chlamydomonas* to approach more closely the ancestral form than any of the colonial genera, since colony form is not constant, but varies in every genus.

On the other hand, one might argue that as colonies of some sort occur in most of the genera, one would expect them in the ancestors. It is true that they all descend from a common colonial ancestor[1], of the *Gonium* type, if the series be correct, but if this be admitted it is equally justifiable to trace them back to a unicellular ancestry. For it is impossible in theory to draw the line at any one point although for practical purposes such a line is convenient. There are a number of unicellular genera related to *Chlamydomonas* and having more in common with it than the colonial forms. If *Chlamydomonas* be taken into the series, these other forms, which differ little from it, must be considered.

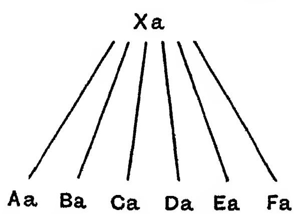
[1] And more remotely from unicells.

Unfortunately the differences between species have not been subject to exact measurement. To do so would be to delimit the species artificially. As the species of taxonomy are artificial units there is no reason why this should not be done. The use of artificial units has succeeded very well in physics, and there is no reason to believe that it would not be equally successful in biology. The question of the selection and measurement of characters will be considered later. But systematic affinity, once the species are defined, is a measureable entity. It will necessarily be of a statistical nature like the results of Mendelism and biometry. But owing to the great variety of characters and species it has not yet assumed a mathematical form. And further, like other statistical results it will not express absolute truth, the degree of accuracy depending on the number of characters taken into account and the number of species with which the subject species is compared. In short, in determining relationships, the actual composition of the natural system must be taken into account. Whilst it is possible to isolate a part of the natural system and discuss its phylogeny, it is not possible to isolate a number of forms which differ from one another within certain limits and then exclude large numbers of certain stages which are known to exist within these limits. If this is done we are in a worse position than if the group were scarcely known, for in the latter case we should still believe that the known members were fairly representative of the group. If we agree to consider the colonial members only of the Chlamydomonads then clearly the ancestor was a colonial form, but if unicellular genera of Chlamydomonads be considered as well as colonial ones account must be taken of all the known genera or at least a representative number of them. Of course it follows from this that the phylogeny of the genera of a group can only be discovered when a considerable number can be taken into account; the more numerous the types available for comparison the more certain the phylogeny becomes. The phylogeny of small groups of genera can be suggested by analogy with large ones, but in the investigation of small groups the phylogeny of species rather than of genera should be studied.

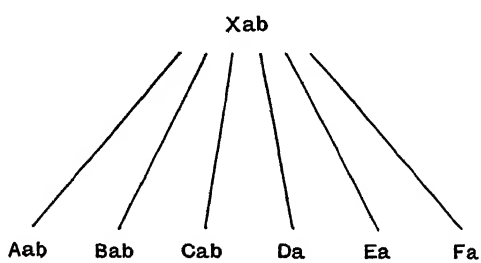
Any group of related species, except those which are due to mere Mendelian recombination and which are discussed elsewhere, can be conceived as descended from a single common ancestral species. That does not prove, of course, that there were fewer and fewer species in the more and more remote periods of the earth's history, for, as is well known, the majority of the species of past floras and faunas are now extinct. A few species only pass on offspring from one geological epoch to the next, but from these few the earth is stocked with forms, pre-

sumably as varied as in the previous age. Suppose a group of living species to have descended from a common ancestor. All these species differ among themselves and from the ancestral species, but if any character or characters be considered in the supposed ancestral species, then some of the derived species will approach more nearly to the former in this particular character or characters. Now if a number of the living species exist it is possible to tell by comparing them which most closely approach the ancestral species in any particular character or characters, since the average members of the group, in respect to that particular character or characters, will be the most like the parental species. Another fallacy, however, might easily creep in here when we come to apply this principle to certain particular cases. Strictly it should only be applied to groups of which the members *all* have a certain character or characters constantly present, since it is only of such groups that we can say *a priori* that the members are descended from a common ancestor in each case. The individual groups into which we divide the natural system are, or should be, determined by the results of phyletic investigation. We know at least something of the ancestry if we can select the group, *i.e.* that it possesses the group character.

Let *A*, *B*, *C*, *D*, *E* and *F* represent species possessing a character *a*. If we exclude the possibility of *a* having originated more than once in evolution, a possibility which will be discussed in the next section, then all these species can be regarded as having arisen from an ancestral species *X*, as represented by the following diagram:

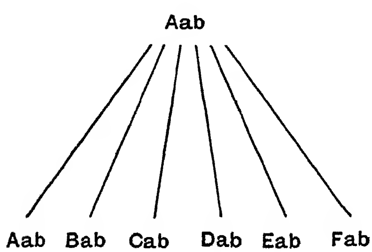


Now suppose that *X* possessed a second character *b* which is present in *A*, *B* and *C* but not in *D*, *E* and *F*, then we obtain the diagram:

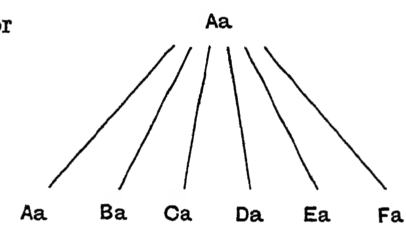


If this represents the facts correctly then it will be impossible to tell from inspection of the living genera only whether the ancestral species *X* possessed the character *b* or did not. But as a matter of fact such a diagram is most unlikely to represent a real phylogenetic relationship. In hardly any systematic group do we find half the members to possess a character which is absent in the other half. Such cases do occur and with regard to the particular character concerned we can say nothing about the ancestry. But far more frequently we find the character predominantly present or absent, viz. *Aab Bab Cab Dab Eab Fab* or *Aa Ba Ca Da Ea Fa*.

Instances of this kind are found for example in the flowering plant families *Umbelliferae* and *Compositae*, each of which has a characteristic type of inflorescence (compound umbel, capitulum) throughout the majority of its members. The possession of the special inflorescence is ascribed to the common ancestry of each family. Yet there are plants, known to be *Umbelliferae* on the basis of many other characters, which do not possess the compound umbel. The genus *Astrantia* is characterised by simple umbels, the genus *Petagmia* by a number of dichasia. In *Xanthosia* and *Azorella* some species show single flowers, in the place of the umbels of allied species. And there are also undoubted Composites, such as *Echinops*, in which the place of the capitulum is taken by a single flower. Many other examples of such aberrant types will occur to the reader. In such cases we can infer the condition of the ancestry by inspection of the living species of the same family, for since the force of heredity is stronger than that of variation the predominant character *b* or absence of that character may be attributed also to the ancestry, thus:



or



In the case of a quantitatively varying character of the same kind, such as number of cells in colony in the *Volvox* series, we can also obtain some indication as to the degree in which it was developed in the ancestry. For if a large number of forms, distinguished on the basis of

other characters, have the character developed to a given extent, then the character was probably present to that extent in a relatively late stage in the ancestry. A good example of this has already been seen in the series of colonial Chlamydomonads quoted above. For the different grades of colonial development are each represented by one generic type[1] and few specific types, while the related unicellular forms are so diverse as to have been long known to be representative of numerous genera. And even the division into genera is scarcely a measure of their true variation, since the genus *Chlamydomonas* itself embraces a very varied assortment of species, and from the point of view of life history should undoubtedly be sub-divided.

It is thus possible to state definitely, not only that the natural system is a reality which can be described in the same way as a material system, but also that it gives true information as to phylogeny, though such information must be incomplete and may be synthesised by means of the imagination as we shall see in the last section. If however the preceding methods are borne in mind, phylogeny will contain information as well as hypothesis. Nevertheless it is not the purpose of this work to discourage the formation of hypotheses, provided the latter are built up by the synthesis of our actual knowledge. It is most improbable that our knowledge of the course of phylogenesis of any one group will ever be complete, and to do without hypotheses would be as unthinkable in phylogeny as in any other science.

IV. Convergence.

In the previous section it has been assumed that resemblance is a measure of genetic relationship. But every comparative anatomist knows many instances of close similarity between organisms, or parts of organisms that are not thought to be closely related; for only a particular kind of resemblance, or resemblance under certain circumstances is considered indicative of community of descent. Affinity was distinguished from mere similarity early in the history of classification. Linnaeus himself had made the distinction, and the idea was also clearly expressed by C. Agardh in 1825 (1). Linnaeus is credited with the aphorism "that the characters do not make the genus, but that the genus gives the characters," a saying which Darwin (29) interpreted as one of the many

[1] *Volvox* has recently been sub-divided into several genera by W. R. Shaw (103). This supports the view, advanced elsewhere (20) and discussed later, that *Volvox* or at least some of its species do not belong to the same series as the other colonial Chlamydomonads.

expressions of the opinion that "some deeper bond is included in our classifications than mere resemblance." That the aphorism had however been understood in some other sense is evident from the fact that Agardh (1) pointed out that the affinities of species were deducible from their characters, not *vice versa*, a statement showing that one of the fallacies regarding phyletic series which still occasionally appears in the literature of to-day had already been foreshadowed and controverted.

In 1843 Owen distinguished between homology and analogy; the determination of the difference between these two conditions resting on anatomical comparison. In the Darwinian period the real cause of the distinction between resemblance and affinity became clear. Darwin, following Owen, spoke of analogy and homology. Later, Ray Lankester (67) pointed out that many of the supposed homologies were really cases of particularly close analogy, which he called homoplasy. The true homology of other authors is spoken of by this author as homogeny. Haeckel (49) and Gegenbaur (44) stated that phyletic relationship can be traced by the study of homology, the latter author adding that our knowledge of blood-relationship is directly proportional to the certainty with which homology has been established in any particular case. The proof of homology of course depends finally upon detailed anatomical examination.

Not only was there a pre-Darwinian distinction between homology and analogy, but even now the distinction is in the first place an inference from the facts of systematic morphology, not an evolutionary conception forced on them, although we now give an evolutionary interpretation of the facts. A few simple examples will be sufficient to show that one might know nothing of the theory of evolution and yet be acquainted with the facts of convergence in the natural system. All fully developed plant parasites and saprophytes, for example, have something in common, even if it only be the absence of chlorophyll. But a very little morphological study shows that they belong to different groups to judge by the sum of their characters. In some early systems of classification the parasitic and saprophytic habits played an important part. Lindley assigned the most aberrant types (70) to a special class. In Endlicher's system (38) not only were the *Thallophyta* divided into *Protophyta* and *Hysterophyta*, roughly equivalent to the modern Algae and Fungi, but the most extreme flowering parasites are placed apart from the flowering plants in a division *Hysterophyta* of the *Acrobrya*. To-day these colourless forms are universally admitted into orders containing green Dicotyledons. But even before the idea of phylogenesis had been

evolved, the true affinities of some of these parasites had been detected. Fries (39), for example, places the *Balanophoreae* in a division of Dicotyledons containing *Aristolochiae* and *Urticaceae*. The extreme parasites amongst flowering plants offer examples of particularly close convergence with an extremely widely separated group, the *Fungi*, the whole vegetative system of the *Rafflesiaceae*, as is well known, being little more than a mycelium, with no trace of differentiation of stem, root and leaves. In animals many similar instances could be given; the function of flight, and hence the evolution of wings having appeared in groups with not the remotest connection with one another[1]. The resemblance in body form between Whales and Fishes is another well-known instance.

In a number of characters, Bats resemble Birds more closely than they do Whales. Suppose an absolutely uncritical view of resemblance be taken and such characters as size, weight and external form be taken into account. Then Bats must be classed with Birds and not with Whales. Yet zoologists believe that Bats have a greater affinity with Whales than they have with Birds; that the common type, from which both Bats and Whales are derived, is less remote than that from which Bats and Birds are descended. At least this is the idea now supposed to be expressed by saying that both Bats and Whales belong to the class *Mammalia*, whereas Birds belong to a different class, *Aves*. Yet the true systematic position of Bats was known long before evolution was accepted. It simply resulted from the fact that the attempt to compare the parts of Bats and Whales meets with greater success than the attempt to compare Bats and Birds. The plan is similar in the former case, even if the actual individual resemblances in other characters are few. The reason why structure is important, whilst other characters such as size, weight and colour are very insignificant in taxonomy, depends on certain general facts, relating to the distribution of characters, which will be considered subsequently. But if these characters, which are unimportant in taxonomy, can be developed independently in evolution, it can be questioned as to whether resemblances of all kinds may not be derived from other than genetic relationships.

In all the examples so far given, moreover, there is obviously a very great difference between homology and analogy. But homology and analogy may be of different kinds and in some cases it may be difficult to distinguish between them. St G. Mivart (85) has enumerated over twenty different kinds of homology, including however a number of cases that are probably analogies. Convergences may be equally varied (116).

[1] *E.g.* insects and bats.

It is not my intention to deal with this difficult and interesting morphological subject here; to do so would be to write a text book of comparative anatomy. Certain facts must however be noted, viz. (i) every anatomist believes in the distinction of homology and analogy; (ii) the existence of homologies is one of the chief proofs of the theory of evolution and not *vice versa*; (iii) the existence of similar structures which anatomists have not yet decided upon, as to whether they are homologous, or analogous, is no proof that homology is not a reality; (iv) innumerable instances of homology, in the narrowest possible sense, exist. The concepts of homology and analogy it is true are concepts of relation, but as Mivart (86) well expressed it long ago: "These perceived relations, though subjective, *as relations*, have nevertheless an objective foundation as real parts, or conditions of parts, of real wholes."

If the proposition, that homology, in the narrow sense (Lankester's homogeny), is a criterion of relationship by descent, does not hold good, the tracing of phylogeny becomes impossible. For there is no means of distinguishing between homology with genetic basis and homology without such basis except by observation of the facts of structure. Some remarkable criticisms of homology as a measure of relationship have been put forward by O. Hertwig (58, 59). This author cannot deny the existence of homology, as deduced from anatomical comparison, but thinks that it may not always indicate community of descent. How then does he explain homology in these other cases? He thinks it may be due to the similarity of the laws governing the evolution of animals. But what do we know of these laws apart from the structures they give rise to? And if similar structures exist, similar laws must have been acting to produce them. The factors determining any given form are partly environmental and partly hereditary. Given the same environmental factors it will be impossible to obtain the same structure, unless the inherited factors are also the same. Thus viewed Hertwig's criticisms fall into line with those that will be discussed subsequently in this section, and which present an apparent difficulty in the tracing of phylogeny; the possibility of a repeated evolutionary production of one and the same group type.

Before considering the extent to which convergence can be traced, an aspect of homology must be considered which has not hitherto received the attention it deserves. It has already been pointed out that a species is defined by an aggregation of those characters which are common to a vast number of individuals, and these characters naturally occur together in what are generally called stages in the life history.

Just as the different organs of any one stage are arranged together in a particular way, so the different stages are collected together in a series, the ontogenesis. It is obvious that ontogenetic homology, *i.e.* the correspondence of phases of the life history, is of the greatest importance, if homology has any value at all, in establishing genetic relationship.

As an example of the apparent diversity of forms of homologous ontogenesis we may consider the *Isokontae*, a class of Green Algae. All these have certain common characters, mostly cytological, such as the presence of two equal flagella in the zoospore stage, and the formation of starch. Even the nuclear characters were found to be characteristic in a number of diverse members of the group by von Neuenstein (88). Yet externally the various *Isokontae* differ in a remarkable manner. The *Polyblepharidaceae* are typical Flagellates, and reproduction occurs in the motile stage. In the *Chlamydomonadaceae* the motile stage is the predominant one in the life history; the organism is generally found swimming about actively. But at division it withdraws its cilia and divides in the resting state. Hence we can distinguish the motile stage (= zoospore) from the sporangium stage. In the *Tetrasporaceae* and *Chlorococcaceae* we can distinguish zoospore, sporangium and palmella stage. The sporangium is dominant in the *Chlorococcaceae*, the palmella in the *Tetrasporaceae*. In the *Ulotrichaceae* the filament is the dominant phase, but the cells of these can take on the sporangial form and produce zoospores. The zoospores may frequently deviate into a palmella state. So in the *Ulotrichaceae* at least four distinct stages of the life history can be observed, and three of these are homologous with the phases described above. Branching of the filaments may lead to further complications but many of these "higher" forms have been observed to pass through the "lower" states in the development of their complicated thalli.

A large number of very excellent cases of convergence in evolution have been brought together by Willey (116). These include not only convergences in structure to which alone the author confines the term homoplasy, and which had previously been the only well-known examples of convergence, but Willey has shown that convergence extends to habit and function of nearly every kind, and is widespread in every group of the animal kingdom. One may add it is equally well established in plants. It is certain that heterospory, and probable that even the seed habit, have been developed more than once in the history of the vegetable kingdom. But perhaps one of the most amazing cases of

convergence leading to parallel development of groups in plants has recently been found among the Algae owing to the extensive work of Pascher. The older writers mostly divided the Algae into six classes, which were given various names, but can best be indicated by those accepted by various of the older algologists, viz. *Chlorophyceae*, or Green Algae, *Cyanophyceae*, or Blue-green Algae, *Rhodophyceae* or Red Algae, *Phaeophyceae* or Brown Algae, *Bacillariophyceae* or Diatoms and *Charaphyceae* or Charads. Modern conceptions of the classification of this phylum have been brought about by an investigation of the Flagellata. It had been known for some time that a special order of the *Chlorophyceae*, known as the *Confervales*, had a number of special cytological characters, particularly in their yellow-green colour, their bivalved cell wall and the inequality of the two flagella of their zoospore, when A. Luther (79) in 1899 showed that certain Flagellates (*Chloromonadineae*) had corresponding cytological characters. He proposed therefore to create a new class, *Heterokontae*, for these Algae and Flagellates. In 1901, K. Bohlin (9) put forward the view that the *Chlorophyceae* are descended from unknown green Flagellata. The zoospores are embryonal forms, representing these ancestors. They possess, like the sperms, two equal flagella. The *Heterokontae* of Luther was accepted and another class segregated from the *Chlorophyceae*; the *Glaucophyceae*, blue-green like the *Cyanophyceae*, but unlike the latter provided with a nucleus and producing starch. This third class was thought to be descended from Flagellates of the order *Cryptomonadineae*. In 1902 F. F. Blackman and A. G. Tansley (7) revised the classification of the Green Algae, accepting the new classes proposed by Luther and by Bohlin, but showing that the *Chlorophyceae* were separable into three classes: *Isokontae* with zoospores having two equal flagella, *Stephanokontae* with zoospores having a crown of cilia, and *Akontae* with no zoospores. The *Isokontae* were shown to contain semi-flagellate forms (*Polyblepharideae*), but the other two classes are without flagellate representatives. The principle of a special flagellate affinity for each algal group has been accepted by morphologists. F. Cavers (17) gives a review of the earlier views on the subject. Each algal class had its special flagellate families, but opinion was uncertain in some cases as to the exact position of the group. J. P. Lotsy (76) even assigned a Cryptomonad ancestry to the *Rhodophyceae* and *Schizophyta*, and for a long time the Cryptomonad Flagellates were represented as the ancestors of the *Phaeophyceae* (17). From the latter group the *Dinoflagellata* were separated (17) and at first classed with the Cryptomonads. The Dinoflagellates are now thought to give rise

Pascher's System of the Algae (slightly modified).

CHRYSOPHYTA			PHAEOPHYTA		PYRROPHYTA	
CHRYSOPHYCEAE	BACILLARIOPHYCEAE	HETEROKONTAE	—	DESMOKONTAE	CRYPTOPHYCEAE	DINOPHYCEAE
Chrysomonadales	—	Heterochloridales	—	Desmomonadales	Cryptomonadales	Dinoflagellatae
Chrysocapsales	—	Heterocapsales	—	Desmocapsales	Phaeocapsales	Dinocapsales
Chrysophaerales	—	Heterococcales	—	?	Cryptoccocales	Dinococcales
Chrysotrichales	—	Heterotrichales	—	?	Cryptotrichales	Dinotrichales
—	—	Heterosiphonales	—			

(*continued*)

CHLOROPHYTA			?	?
ISOKONTAE	STEPHANOKONTAE	AKONTAE	EUGLENINAE	CHLOROMONADINAE
Volvocales	—	—	—	—
Tetrasporales	—	—	—	—
Chlorococcales	—	—	—	—
Ulotrichales	Oedogoniales	—	—	—
Siphonales	—	Conjugales	—	—
Siphonocladiales	—	—	—	—

to their own algal representatives and are probably biphyletic (89), whilst a special series of algal forms is connected with the *Cryptomonadales* (89). The scheme of Pascher's recent system of classification (89) is shown here in slightly modified form[1]. It will be seen that his classes are arranged in larger groups which may perhaps be ranked as phyla.

From the point of view of phylogenetic theory the history of these discoveries is instructive. A criticism that might readily be made is that if such gigantic changes can be made in a relatively short time, the whole system is unstable. And many authors would not accept all Pascher's conclusions. The older classifications were however not without value; the new system being superior only in that it takes into account more detail of structure than the old. Pascher points out that the modern Flagellates are not to be considered the ancestral forms. However, they represent them to some extent. And there is no doubt that the Cryptomonads do represent, as shown in the older systems of classification, the ancestral forms of the *Phaeophyceae* in certain characters, *e.g.* asymmetrical organisation. But they undoubtedly represent, much more closely, *i.e.* in many of their characters, the ancestral forms of *Cryptophyceae*.

Pascher's system of the Algae, however, is of significance in another way. If it is accepted, then although the general resemblance of the flagellate groups constituting the first horizontal series in the diagram may be explained as due to their actual genetic relationship, the algal groups must have evolved, independently, from the ancestral form of each group of Flagellates. They thus constitute a remarkable example of convergence, not only of individual species, but even of classes. The process might well be termed "parallelism" if that term had not already been used in the literature (19) to signify the special parallelism of ontogeny with phylogeny. No less than six classes show both algal and flagellate representatives and there is little doubt that the *Phaeophyceae*, and probably also at least the *Stephanokontae*, had flagellate representatives, whilst convergence is also found among the various types of Flagellates themselves (17). Other examples of similar phenomena could be cited.

Probably equally good cases could be made for the polyphyletic origin of the fixed phase of many animal phyla. It is noteworthy that each phylum of animals has its sedentary members, not excluding the Chordata if the Tunicates are admitted into this group.

[1] Pascher treats the Stephanokontae and Isokontae as sub-divisions of one class —*Chlorophyceae*.

In the consideration of such an extreme case of polyphyletism as that of the Algae the question arises: if each flagellate group has given rise to an algal group, cannot a single flagellate group have given rise to identical algal forms on more than one occasion? Obviously this can be so. The identical algal class can arise on more than one occasion, but only from identical ancestors, since if the inherited factors are different the resulting progeny will be different.

Pascher (91) has given evidence for the convergent evolution of Rhizopods from different groups of Flagellates. Amongst lower plant types the *Cyanophyceae* offer many excellent instances. These I have discussed in a previous publication (26), and pointed out that they are even more significant than many of the other cases that have been studied, inasmuch as throughout the group the cytological structure is remarkably unlike that of other algae. They therefore afford more certain evidence of homoplasy than any of the other algal groups. The Bacteria, too, are remarkably like the *Cyanophyceae* in organisation, but for a long time it was doubtful whether this was not due to true homology. Bessey (5) even placed a number of bacterial genera: *Sarcina, Beggiatoa, Bacillus, Vibrio, Leuconostoc,* and *Micrococcus* within the families of *Cyanophyceae*. To test this question I made an examination (22) of one of the best known cases of resemblance of a bacterium to the *Cyanophyceae*, viz. *Leuconostoc*, a genus which appears, as is indicated by its name, to be a colourless derivative of the *Cyanophyceae*. It was shown however that in this case the resemblance, although close, was due to homoplasy.

To those who hold that the existence of homoplasy is fatal to the reconstruction of the history of the group, this is sufficient to indicate that nothing can be known of the history of the phyla themselves or even of the classes of a single phylum in which convergence is seen. If cases of convergence could only be found in the characters of the main sub-divisions of very large groups, such as phyla, or classes, these critics might still believe that the phylogeny of smaller groups is traceable.

But if the existence of homoplasy is an objection to phylogeny at all the objection cannot in theory be limited to any particular kind of characters. It might be that homoplasy occurred widely in the characters of small groups such as families and genera. Lotsy (77) even suggested that species might have a polyphyletic origin: his reasons for this being discussed in a later section on Mendelism. This possibility of homoplasy of small groups was foreseen by W. H. Lang (68), and forms the basis for a criticism of the phylogenetic method in morphology.

It is therefore of very great theoretical interest to show that convergence occurs in small systematic groups. For a long time the series of colonial Phytoflagellates discussed in the previous section was looked upon as an almost perfect example of a phylogenetic series within a small group. Yet there are reasons to believe that even in this small group parallelism occurs. For reasons which I published in 1918 (20) I cannot believe that the simple phyletic series, as constructed in the previous section, is a correct representation of the facts. Further, in a more recent note (27) it was pointed out that, owing to the homology of sporangia with colonies, the character on which colony formation depends in *Volvox* is more closely paralleled in one of the unicellular genera than in the other colonial forms. The scheme may be represented thus:

	Eudorina	
	|	
	Pandorina	
Colonial	|	
	Gonium	*Volvox*
....	|	|
Unicellular	*Chlamydomonas*	*Sphaerella*

The object of the publications mentioned was to trace the relationships of the colonial Chlamydomonads, it being assumed that a natural system is to be arrived at by morphological comparison of species or forms. The changes that were suggested in the current classification of these organisms however raise the important question: is there any possibility in framing a phylogenetic system of classification at all? And the same doubt arises in the case of the Elephants. They undoubtedly show parallel evolution (32) if specific as well as generic characters are considered. If, then, such excellent phylogenetic series as those described in the last section do not bear the test of intensive morphological examination, and if groups of merely a few genera can be interpreted as polyphyletic, what possibility is there of ever arriving at a satisfactory grouping from the phylogenetic point of view? If one doubts the possibility of a phylogenetic interpretation of the natural system because of the parallel development of great groups, still more must one doubt this possibility in view of cases like the one cited.

Now there is abundant evidence from some of the lower groups of organisms for homoplasy within small groups, as well as for the more general parallelism above cited. It might be expected that cases of convergence would be more difficult to detect in the lower organisms since they have fewer structural characters. In the higher organisms, *i.e.* those with very numerous and highly differentiated parts, con-

vergence in one part may be detected by fundamental differences in all the other parts. But in the lower organisms with few visible characters this would often be difficult. Nevertheless in recent years a number of cases have been put forward and, although some of them have not been rigidly proved, they all indicate very strongly the possibility of homoplasy within very small systematic groups.

An extremely strong probability of the polyphyletic origin of genera is suggested in the group of the Desmids by an observation which I have recorded elsewhere (24). The genus *Arthrodesmus* is characterised by cells which show, amongst other features, a fusiform or elliptical form in vertical view. Certain forms resembling *Arthrodesmus Incus* Breb. in every respect, except in being triangular in end view, are known. These are sometimes considered as mere variants of this species, sometimes as an independent species. They ought to be placed, in the accepted system of classification, in the genus *Staurastrum* which has radial structure in end view, and no doubt they would have been described as a species of this genus had it not been for the close resemblance in all other characters to *Arthrodesmus Incus* Breb. These forms illustrate, then, the transition from the dimerous to the trimerous type of symmetry. Now I have shown that a trimerous form which is equally similar to another species, *A. convergens* Ehrenb., exists and is in fact found in association with it. Clearly the transition from dimery to trimery or *vice versa* may occur independently and the genus *Staurastrum* for example may have had a polyphyletic origin. But the facts do not destroy the possibility of a system of monophyletic genera, but rather suggest the inadequacy of the present scheme of classification.

Still more remarkable are those cases in which a species at one stage of its life history passes through a transitory form which is very similar to, or even apparently identical with, the more permanent form of another species. Cases of this kind are quite well established in many Green Algae of the class *Isokontae*. In some it may be due to a kind of excessive variation, genetic or otherwise, not closely related to variations in the conditions since the variant forms may be found along with the typical ones. The Green Alga *Gloeococcus Schroeteri* is one of the commonest constituents of freshwater plankton in all parts of the world. It normally consists of globes of mucus containing a variable number of cells. The question of its variation has been studied a little more than that of most other members. It is known to be very variable, and Chodat had discovered that it passes into a stage similar to that of the genus *Tetraspora*, *i.e.* a large irregular mass of mucilage with high cell content but

lacking the pseudocilia of this latter genus. An examination of a large number of specimens from Ceylon (24) shows that it also has a few celled stages in which it resembles the allied genus *Eudorinella* except in its absence of flagella.

We have only to imagine the acquisition of pseudocilia by the large form, or of flagella by the small form and we find it impossible to separate this species from two others belonging to two different genera. Of course we may not be willing to admit that such imaginary steps can be taken in nature, but as a matter of fact in the still more simple group, *Cyanophyceae*, there is abundant evidence for the complete transition of species living together.

The genus *Microcystis* contains some of the largest colonial members of the *Cyanophyceae*. Many species attain a very great abundance in the freshwater plankton and at certain times of the year give rise to "water-bloom." They are even more abundant in the tropics than in our climate. As has been pointed out elsewhere (23) two species show a remarkable homoplasy with simple colonial forms of *Tetrasporaceae*, which however belong, as shown by their entirely different cell characters, to a totally distinct class, *Isokontae*. But the species are chiefly of interest here because something is definitely known of their variation. They show what may be interpreted as a homoplasy within the genus, *e.g.* the clathrate character of the colony occurs in species not otherwise closely related (*M. aeruginosa* Kuetz. and *M. holsatica* Lemm.), whilst the species *M. pseudofilamentosa* Crow has elongated, segmented colonies as in *M. stagnalis* Lemm. but is otherwise much more closely allied to *M. aeruginosa* Kuetz. and *M. flos-aquae* (Wittr.) Kirchner.

It is unnecessary to discuss here the question as to whether the different morphological types that can be distinguished are really species or varieties. It is certain, however, that colony form tends to be inherited in the genus, under constant conditions, as the author has shown in cultures (26). Yet in these organisms the colony will vary to an extraordinary degree (26). In nature there are numerous transitional forms so that the distinction between species is purely one of convenience. There is nothing to disprove that the whole genus consists of a single species which is very variable, but if this view is taken one might equally well include many other forms, such as *Coelosphaerium dubium* and many species of *Aphanocapsa*. And the latter show transitions with many other genera of *Cyanophyceae*, so that we might on the same basis include perhaps the bulk of the *Chroococcaceae* and *Chamaesiphonaceae*. In culture *Microcystis* certainly takes on an *Aphanocapsa* form under

unfavourable conditions (26). Similar conditions are suggested in other *Cyanophyceae* (26). They occur to a less extent in the Green Algal classes, *Isokontae* and *Akontae* (25), but are by no means unknown even in higher organisms.

The connection of these facts with the question of parallel development lies in the fact that they suggest a polyphyletic origin even for a species. If in nature it is impossible to identify a species without examining its variation or a particular habitat, if the extreme variants of what is supposed to be one species might equally well be placed in another, and if in culture one species can vary even beyond the limits of the genus, then is it not extremely probable that what is called a species, *i.e.* a conveniently distinguishable morphological type breeding on an average true, has originated and persisted for more than one generation not once but many times, probably many millions of times? And if so then is it not quite impossible to tabulate the phylogeny of these species?

An attempt to give a decidedly negative answer to the above question will be made in a subsequent section. To recapitulate the argument outlined above, however, and the conclusion to which it has led, it can be stated that convergence, resulting in parallel evolution, instead of radiating evolution, is suspected as soon as the methods outlined for the construction of a phyletic series are applied in detail. It has been shown that a number of large groups (classes) may show remarkable parallels in their individual species and in their classification as a whole. The same is true even of small groups of genera. W. H. Lang (68) has commented on the fact that in the history of phylogeny monophyletic derivations have largely given place to polyphyletic ones. This author seems to think this is an argument against the general validity of phylogenetic conclusions. O. Hertwig (58, 59) believes that homology may occur without indicating relationship by descent. An examination of the facts gives absolutely no warrant for such an assumption. The fact that heredity is an important factor in the formation of any living structure suggests on the other hand that identity of structure means identity of ancestry. That a similar group may originate from similar ancestors in a polyphyletic manner, *e.g.* Algae from Flagellates, does indicate that the same group can originate from the *same* ancestors on more than one, possibly on many, occasions. This kind of "polyphyletism" is not confined to large groups. It is found in small groups, commonly supposed to be monophyletic, and therefore is of great significance in phylogeny.

V. Regression.

In considering the existence of series in the natural system, it was found that these series may possess a definite direction. This direction was considered to resemble, although not to be identical with the direction of phylogenesis, because it consists of linear relations as opposed to collateral. And if the natural system be taken as a whole it can be said that a large number of series exist leading away from the unicellular organisms, although not necessarily connected by all the links that might be imagined. This conception of the unicellular organisms forming a central group, and thus representing the primitive forms of life, depends on the fact that all the higher organisms are built up of cells, and if the cellular character is common to all the higher organisms it must be explained as an ancestral inheritance. On the other hand, the way in which the cells are built up into higher morphological categories differs in the different groups, and hence it is improbable that any method of cell union was present in the most remote ancestors, *i.e.* the most remote ancestors of all living phyla were unicells. When we find also that one stage of practically all organisms, viz. the fertilised egg, is unicellular, it becomes practically certain that such a stage is the one that has persisted from the most remote epochs, whereas the other stages of the life history, which are different in different groups, are a later acquisition.

It is not our object here to defend in detail the so-called biogenetic law[1], or law of recapitulation of phylogenesis by ontogenesis. However, the question cannot be avoided here as the basis for a discussion of what is frequently called reduction in evolution, or, to use a less ambiguous term, regression. It is obvious that the regression of a group to its ancestral condition, if it occurs, introduces a factor into the study of phylogeny as perplexing as that met with in convergence.

If embryonic, as well as adult characters, are considered it is found that the former are generally common to larger groups than the latter. Just in the same way as any other characters common to a group were probably present in the ancestors of that group, the majority of embryonic characters appear to be ancestral in the majority of species. When however a special embryonic character not occurring throughout the group is met with, it cannot be considered as ancestral, any more than an adult character occurring only in a special sub-division of a

[1] For an account of the different variants of this law see E. G. Russell (98).

group cannot be ranked as ancestral to the whole group. Thus the placenta which occurs throughout the sub-class Placentalia of the mammals is ancestral for that group, is not common to the Vertebrates as a whole and is therefore not ancestral for the latter. In view of the enormous range of certain simple embryonic forms, *i.e.* the unicellular stage in plants and animals, the gastrula stage in many animal groups, and the filament in the early stage of many plants; and taking into account the probability that the embryonic characters would tend to vary as well as the adult characters, it is extremely probable that these embryonic characters represent the ancestral characters of these very large groups.

The truth of the biogenetic law becomes obvious if embryonic characters are considered as well as adult characters. The law is then seen to be a conclusion derived from comparative morphology, and not an evolutionary conception forced on them as some authors would have us believe. Of course, the embryonic characters must be sought for in the corresponding embryonic stage of the ancestor, but, as the adult characters are often so variable in different species of the same group, it may be greatly doubted whether the part of the life history called the adult phase in the living forms was represented in the common ancestor at all.

Darwin (29), of course, explained the general comparative constancy of embryonic characters throughout large groups as due to the lesser action of natural selection on the early stages of the life history. It is doubtful whether this explanation holds good, if one takes into account the high degree of mortality of embryos. At the same time his explanation does not necessarily contradict the phyletic conclusions referred to above; it merely explains the mechanism by which the embryonic characters have remained constant in contrast with the adult characters.

The resemblance of embryos was first noted by Von Baer (113), who seems to have recognised the main principle of the biogenetic law, as outlined above. The most serious criticisms of the law depend on the fact that embryos are not really alike (98). W. His (60) pointed out that even in external form embryos are not really alike. A. Sedgwick (102) and O. Hertwig (58) have also insisted on the specificity of embryos. What all these authors seem to forget is, that relatively to the adult state the embryo is comparatively constant in the majority of groups[1].

[1] This is true even of plants. B. Sahni has shown (99) that recapitulation applies to plants. See also Gates (42).

Their criticisms are an excellent example of a common error in morphology of concentration on detail, excellent as it is in itself, leading to a blindness to the more obvious features.

A species may represent an ancestral form in some character or characters, but not in others. The organisms possessing as the main phase of their life history characters which are constantly exhibited by the early embryo of the other groups, *i.e.* the Protista or unicellular organisms, certain simple types of Metazoa and the filamentous Algae and Fungi among plants therefore represent the ancestral, the earliest stages in evolution. But because they represent, in certain definite characters, these ancestral stages, they may be very different from the real ancestors. It is a failure to recognise this that has led to much confusion in phyletic schemes. And because we know common embryonic characters and also know living organisms which possess similar characters in the adult phase we are enabled to form a conception of such organisms, notwithstanding the fact that the organisms which possess well developed archaic characters may at the same time be highly differentiated along some lines, as many of the modern Protozoa undoubtedly are. Phylogeny can give little satisfaction to those who desire absolute truth, but those who hold a partial view to be better than none at all may find it an interesting study.

However it must still be decided whether a phylogenetic table of a group can be constructed in the light of the above facts.

Suppose a given species to be defined as possessing the characters a, b, c and d. Suppose in the course of phylogenesis this species, gives rise to another species somewhat modified. Let the modifications, *i.e.* the specific difference between the parent and offspring species, be represented by e. Theoretically all cases can be represented in this way, even the complete disappearance of one of the characters a, b, c or d if we regard e as an inhibitor of one or more of these characters, although in this case an omission of one of the symbols will be more appropriate. This will be a convenient mode of representing the facts, *i.e.* the observed characters of two species, and is not meant to imply any Mendelian factors. Now suppose a third species arises from the second, this can be represented by the series of characters $a\,b\,c\,d\,e\,f$. The group can continue to evolve by adding new modifications. Suppose however that these new modifications consist of loss or inhibition of some of the old characters. This can take place (i) with or (ii) without addition of new characters g, h, viz.

$$
\begin{array}{llcll}
 & \text{(i)} & \qquad & & \text{(ii)}\\
1 & a\,b\,c\,d & & 1 & a\,b\,c\,d\\
 & \downarrow & & & \downarrow\\
2 & a\,b\,c\,d\,e & & 2 & a\,b\,c\,d\,e\\
 & \downarrow & & & \downarrow\\
3 & a\,b\,c\,d\,e\,f & & 3 & a\,b\,c\,d\,e\,f\\
 & \downarrow & & & \downarrow\\
4 & a\,b\,c\,d\,e & & 4 & a\,b\,c\,d\,e\,g\\
 & \downarrow & & & \downarrow\\
5 & a\,b\,c\,d & & 5 & a\,b\,c\,d\,g\,h
\end{array}
$$

In case (i) species 5 will be identical with the ancestral species 1, and species 4 will be identical with ancestral species 2; in the case (ii) species 5 will represent ancestral species 1 in lacking characters *e* and *f*, species 4 will represent ancestral species 2 in lacking *f*. In actual fact we cannot know the linear series represented in the above diagrams unless particularly favourable fossil material is available. We may know a collateral series representing the supposed linear series, but all the ancestral species may be more or less modified by the introduction of new characters which may be symbolised by the introduction of factors *w*, *x*, *y*, *z*. Thus the known species form the two possible collateral series:

(i)	1 *abcdw*,	2 *abcdex*,	3 *abcdefy*,	4 *abcdez*,	5 *abcd*
(ii)	1 *abcdw*,	2 *abcdex*,	3 *abcdefy*,	4 *abcdegz*,	5 *abcdgh*

In the first of these series if *x* is identical with *z* then the two species 2 and 4 will be identical. Such series are of a kind familiar to all systematists. The characters *w*, *x*, *y* and *z* suggest no sort of seriation; on the other hand the characters *a*, *b*, *c*, *d*, *e* and *f* undoubtedly do suggest seriation. Characters *w*, *x*, *y* and *z* will be neglected in tracing descent. Then only the linear series (i) and (ii) need be considered. The phylogeny of (i) will be represented:

$$
\begin{array}{ll}
1 & abcd\\
 & \downarrow\\
2 & abcde\\
 & \downarrow\\
3 & abcdef
\end{array}
$$

of (ii)

$$
\begin{array}{ll}
1 & abcd\\
 & \downarrow\\
2 & abcde\\
 & \downarrow\\
3 & abcdef\\
 & \downarrow\\
4 & abcdeg\\
 & \downarrow\\
5 & abcdgh
\end{array}
$$

It is to be noted that if species 5 were unknown it would be impossible to decide the relative positions of species 3 and 4 in (ii). In the series (i) the phylogenetic table does not actually represent the full history of

the group, because species *abcd* has actually appeared twice in time. This however would be unknown as far as the characters dealt with in the table are concerned. And as phylogeny is an arrangement of species or other groups, *i.e.* aggregates of characters, it cannot be expected to show the origin of the members constituting that group. To anticipate for a moment the conclusions of a later section it must be admitted that for purposes of phylogeny the species *abcd*, *abcde* and *abcdef* must be considered as units, and the only way of representing their phylogeny is as above.

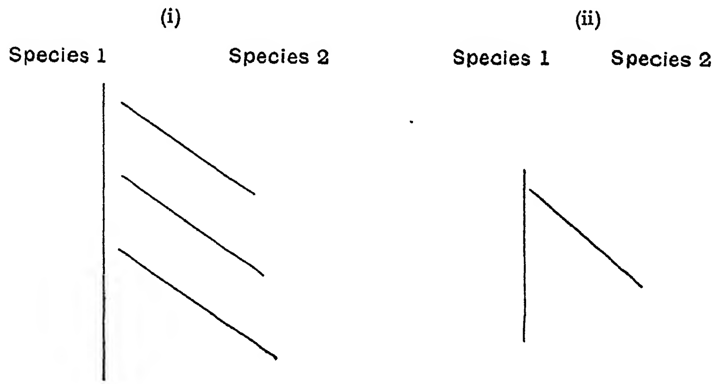
It is true that in palaeontology evidence relating to the actual history of a group may be obtained. But examples of reversible series such as *abcd* → *abcde* → *abcdef* → *abcde* → *abcd* do not appear to have been met with. In fact palaeontologists have gone so far as to maintain there is a law of irreversible evolution, even for the parts of an organism (94).

A recent attempt to show reversible evolution is based on embryological considerations. G. A. Boulenger (10), by a study of the fish family *Cichlidae* having both conical and bi- or tri-cusped tooth types, concludes the primitive type of tooth was undoubtedly conical. In some African species of this family bi- or tri-cuspid teeth are met with in young fishes, conical in the adult, and the author maintains that evolution is, in these species, now retrogressive towards the conical type. The author also believes that the number of vertebrae in this group at first decreased and then increased in number. This author has also indicated a similar case of reversed ontogeny in the lizard genus *Eremias* (11). But these conclusions are arrived at by the ordinary methods of morphological comparison, and do not invalidate the methods themselves. In characters other than those cited there is undoubtedly progression.

However, palaeontologists appear to have discovered something which is equally confusing to the phylogenist as extensive reversible evolution would be. A lineage may be defined as a species which can be traced through successive geological periods. Changes are observed in the morphology as the successive stages in a lineage are examined. These changes are generally admitted to be gradual, and hence, according to A. E. Trueman (112), the stages cannot be admitted to be distinct species. The existence of continuity between forms cannot be held as a criterion for placing forms in one and the same species, however, and there is no other reason for supposing that the differences observed between successive stages of the same lineage differ in any other way than living species do amongst themselves. In fact the successive stages of a lineage have received distinct generic names. Trueman cites as an

example the lineage of the mollusc *Gryphaea incurva* from the lower Lias. This group shows various changes in successive horizons. One remarkable change is the increase of coiling, so that progression takes place, in time, from flat shells belonging to the genus *Ostraea* to incurved forms of the genus *Gryphaea*. Many similar lineages are known to palaeontologists, but the remarkable fact about this one and some others is that not only are the various stages found at successive horizons, but also, if a large collection is studied from one horizon, a few variants exactly like those forms which are dominant at other horizons are met with. Trueman thinks therefore that the whole lineage cannot be subdivided. He says: "no divisions that may be made either in the specimens at one horizon or in those of successive horizons, have any objective reality." It is true that the problem of continuous variation introduces complexities into classification which will probably be solved by the use of a numerical scheme such as that suggested by Trueman (112) or by Bernard (4). But the difference between an *Ostraea* and a *Gryphaea* is objective enough. To apply the principle of continuity in living forms, as Trueman does in fossils, would lead to placing whole families of certain groups in a single species, for I have shown (26) that in the Blue-green Algae, for example, as Bernard has in the Stony Corals, that the species are connected by innumerable intermediate links. However, the situation recorded by Trueman, viz. that "the lineage is represented at *each* horizon by forms which exhibit different degrees of acceleration in their progressive characters," several examples of which could be given, not only amongst Lamellibranchs but also amongst Gastropods and simple Corals (112), suggests the possibility that a species may be derived from the same parent species on more than one occasion. For instance, *Gryphaea* may have originated from *Ostraea* independently at several different horizons. The facts do not prove this; various other explanations are possible. Trueman suggests that hybridisation may have played a part. But the possibility of such independent origin of one form from another is not excluded. In fact when one considers large groups there is some evidence of this occurring. It is a form of convergence. But a careful analysis of palaeontological facts bearing on phylogeny made some years ago by Depéret (32) led this author to say "the phenomena of convergence noticed in nearly all fossil animals seem to me to have been singularly exaggerated." He goes on to explain that by appealing to the organisation as a whole the analogies may be detected. In a very small number of cases, particularly in the Ammonites, however, he admits that almost identical forms have been repeatedly produced in the

series of ages. Such repeated products are not simple regression, but from the point of view of phyletic construction they offer a similar difficulty. If the strata are known the history of the series can be constructed as in (i); without it however, if the forms of successive periods are not marked off in one way we are led to formulate a simple phylogeny, deriving the one species from the other.



However, if we are concerned with the origin of the species, not with the individuals composing it, (ii) will be the appropriate representation (see sections VIII and IX).

Many instances of regression in evolution are found in vestigial organs. These frequently occur in otherwise highly differentiated parts and their reduced nature is inferred from this fact. The wings of Penguins, for example, although much less developed than those of most Birds, cannot for a moment be considered as primitive, since they are associated with a structure which belongs to a comparatively advanced group of Birds. The same principle applies to many of the other well-known instances of regression. In some cases, by convergence, the reduced organ may simulate the primitive form of that organ more or less closely. But it is always possible to detect its regressive nature when it is associated with other characters that are highly advanced. In itself reduction in size and number of parts can hardly be spoken of as regression, since such reduction cannot be interpreted as even remotely representing the primitive type in the majority of cases. On the basis of the simplest principles of phylogeny as laid down in the first section of this work, it is clear that among segmented invertebrate animals, for instance, the multi-segmented types are on the whole more primitive than the ones that have few segments. It is among the latter that high

differentiation sets in. And the same applies to the evolution of the flower. The highly differentiated pollen mechanisms are almost always associated with a reduction in the numbers of like parts. And some of the most highly complicated families, like the *Umbelliferae* and *Compositae*, have the smallest individual flowers. It is possible to give instances in which the whole organism is thought to have regressed. The supposition that regression has occurred is here based on a consideration of the life history. Cirripedes afford the best known example of this. The fact that they are regressive Crustacea might perhaps be inferred from a comparison of the adult forms only; that they represent aberrant rather than primitive members of the group would be known from the fact that they in no way represent the typical structure of a Crustacean, although their simplification is undoubtedly a striking anatomical fact. Yet the conclusion that they represent regressive forms is rendered certain when the embryonic characters are taken into account as well as the adult characters. All the members of this group pass through three stages, viz.

Nauplius-larva, *Cypris*-larva, Adult.

Now other Crustacea, *e.g.* *Ostracoda*, are known which pass through the stages:

Nauplius-larva, Adult (*Cypris*-form).

In the general course of their life history, then, the Cirripedes are not simplified. On the contrary they are in this respect more complicated than some other Crustacea. And if the whole of the characters of the organisms are compared, *i.e.* if embryonic characters are taken into account in addition to those of the adult, then there is no reason for even considering the Cirripedes as simplified organisms.

The principle that ontogeny is to be considered in classification will be admitted by all scientific taxonomists, but it is difficult to apply in practice. The life histories are less easy to observe than the adult characters. Yet if the principle is strictly applied great changes will be necessary in our current systems of classification, especially of Protozoa and Thallophyta. It will be recognised that many Fungi and Bacteria are far from being the primitive organisms they have hitherto been supposed. The Mycetozoa are an outstanding example of organisms of comparatively simple anatomical differentiation, possessing at the same time a complex ontogeny. As examples of Protozoa highly differentiated in this way the malaria parasite (*Plasmodium*) and the trypanosomes (*Trypanosomideae*) may be cited. But very many groups of Protozoa

are complicated in this way. The Slime-bacteria (*Myxobacteria*) combine an amazingly simple cytology with a life cycle as complicated as that of the Mycetozoa. Even in the *Haplobacteria*, which are commonly supposed, on the basis of their cytology, to be amongst the simplest of known organisms, the life cycle may be of extreme complexity. This is true of *Azotobacter* for example, according to E. Löhnis and N. R. Smith (75).

A certain simplification has gone on in several phases of the life history in most higher organisms; the way in which this has come about has been studied in detail by Perrier and Gravier (92), who speak of the process as tachygenesis. It will be unnecessary to discuss the question here except to indicate that this kind of reduction is generally accompanied by increasing differentiation in other ways, and can thus be detected. For example, the gametophyte phase is undoubtedly a simpler phase in the flowering plants than in the Pteridophyta, but on the basis of their other characters the former are undoubtedly more advanced than the latter.

It is because authors have sometimes avoided this synthetic view of the organism that they have been able to doubt that we possess a reliable measure for the determination of which organisms are higher and which lower on the scale. Lotsy (77), for instance, expresses this doubt, illustrating it by the statement that Fishes, commonly assumed to be lower than Amphibians, are more highly differentiated than the latter. And so they are in the characters he mentions, but he quite omits to refer to the very obvious features of the life history which show, in the Amphibia, that an entirely new land phase, quite absent from the group of the Fishes, has been added on.

The acceptance of all ontogenetic features, as well as the anatomical characters of the adult, will enable reduced species to be recognised as having a complicated differentiation. It is in fact only in certain characters that the organism is reduced in the cases previously cited. The species taken as a whole has an advanced differentiation. However, the process of regression can go very far, and it is a question whether the regressive can be distinguished from the primitive in certain cases.

As the primitive nature of unicellular organisms has to be taken as a type of phylogenetic conclusions in general, it will be necessary to consider the possibility of a unicellular species being derived from multicellular species by reduction. For this purpose no better example could be found than the extremely common Green Alga *Pleurococcus vulgaris*

Menegh (= *Protococcus viridis* Ag.)[1], responsible for the green dust-like coating on tree trunks and palings in this part of the world. The plant consists of a single cell or a small aggregation of cells, and was for a long time thought to be absolutely typical of the unicellular and colonial family *Chlorococcaceae* which was formerly called *Protococcaceae* on that account. More recently however it has been recognised that *Pleurococcus* has much closer affinities with the filamentous family *Ulotrichaceae*, and that it has probably been derived from the latter by regression (90). The ordinary somatic mode of division of *Pleurococcus* differs from that found in the *Chlorococcaceae*, but resembles that seen in the filamentous *Isokontae*, and in fact in all tissue-forming plants. It takes place by the formation of a transverse septum in the dividing protoplast, separating the two daughter-cells, the lateral walls of which, however, are nothing more than the retained parent membrane. The sporangium and the palmella occur as exceptional modes of division, as in filamentous forms, but filamentous and tissue-forming plants owe their characteristic structure to the predominance of the mode of division just mentioned. On the principle of seriation, as outlined in the first section, it can hardly be doubted that the majority of unicellular forms of *Isokontae* (*e.g. Chlorococcaceae*) represent a stage in phylogenesis before the appearance of the type of cell division, characteristic of the vegetative filaments and tissues of the higher plants. The differences in cytology, and therefore in colony histology, between the vegetative organisation of *Pleurococcus*, and even the palmelloid condition of the majority of unicellular *Isokontae*, are sufficient to show that the genus cannot be placed among the latter as is customary in text books.

The relationship of the genus *Pleurococcus* to the *Ulotrichales* is also suggested by the discovery by Pascher of a species closely allied to

[1] By a study of the original specimens of *Protococcus viridis* Ag., N. Wille (115) has shown that the plants were identical with the exceedingly common species *Pleurococcus vulgaris* Naeg. (=*P. Naegelli* Chod.). Agardh's designation, further, appeared in 1824 and is prior to the other names. In this country it has recently been revived by G. S. West (114). F. E. Fritsch (40) is not in favour of the use of the name *Protococcus*. He points out that its use would lead to confusion, owing to the wide sense in which the term has been used. Those who will admit exceptions to the law of priority should use the term *Pleurococcus* for several reasons. In the older text books *Protococcus* is in general use to indicate *Chlamydomonas* and *Sphaerella*. *Pleurococcus* has little in common with such forms. In the bulk of modern algological literature the term *Pleurococcus* is in general use, and under this name it is familiar to almost every student of biology. The genus does not represent a very primitive type of plant or even of the class to which it belongs, as might be implied by the designation *Protococcus*.

Pleurococcus vulgaris. In the latter the chromatophore is a parietal, basin-shaped structure, but in the new species, *Protococcus annulatus* Pascher (90) or *Pleurococcus annulatus* nov. comb., the chromatophore has, as Pascher indicates, the characteristic ring form typical of the *Ulotrichaceae*.

It is therefore of interest that stages in the life cycle support this. Chodat (18) showed that the organism could exist in filamentous form, apparently thalloid by aggregation of the filaments, and homoplastic with *Protoderma*. It is well known that many members of the *Ulotrichaceae*, such as species of *Stichococcus*, frequently dissociate into chains of a few cells each, sometimes even into single cells. *Pleurococcus* merely represents a further example of this tendency. The fact that division of the cells often takes place in three directions at right angles, rather than in one direction only, is, of course, a peculiar feature of the genus. In this it has retained or regained a primitive feature which in typical filamentous *Isokontae* is relegated to cells which are giving rise to branches, or undergoing special reproductive divisions. The small aggregations of cells comprising the plants of *Pleurococcus* may, in fact, be regarded as highly condensed branched systems. In the *Protoderma* stage this condensation becomes less.

It will thus be seen that if all the characters of *Pleurococcus* now known are taken into account it may very well be ranked as a reduced member of the *Ulotrichales*. But although reduced as far as its normal vegetative characters are concerned, its whole life history, as now known, is by no means simple. Its acceptance as a primitive form depended on ignorance of the characters of the organism as a whole. Even the unicellular stage is, as shown by its structure, only superficially similar to that of primitively unicellular members of the *Isokontae*. It is however an example of regression to primitive forms of *Isokontae* in so far as its most striking characters are concerned. The genus *Pleurococcus* differs in several particulars then from the latter group, and it is, taking its characters as a whole, a complicated organism relatively to the group to which it belongs. We have already shown in an earlier section that the *Isokontae* can be arranged in an ascending series according to the degree of differentiation of the life history. As *Pleurococcus* possesses a secondary unicellular stage in addition to the branched filamentous stage, it must occupy a relatively high position in the series. We can thus enlarge the classification of the *Isokontae* previously given, in the following manner:

Family	Composition of Ontogeny	Dominant Phase
Polyblepharidaceae	Zoospore	Zoospore
Chlamydomonadaceae	Zoospore and sporangium and palmella	Zoospore
Chlorococcaceae	Ditto.	Sporangium
Tetrasporaceae	Ditto.	Palmella
Ulotrichaceae	Zoospore and sporangium and palmella and filament	Filament
Pleurococcaceae	Zoospore and sporangium and palmella and filament and aggregation	Aggregation

Thus it appears that regression is only a special case of increased differentiation. It would not be possible to state that regression to a primitive state never occurs in the descent of species, just as reversion undoubtedly does occur in the descent of individuals. But if it does occur it would not be possible to distinguish the reduced species from primitive ones. They would in fact be the same species and would have been derived ultimately from the same ancestry, and the simplification of phylogeny leads to no confusion. The question must be postponed, however, to a later section for detailed discussion.

Before leaving the question of regression, two facts from geology proving that the lower types have given rise to higher must be referred to. One is that fossils show a seriation of types. Among the vertebrates Fishes appear before Reptiles, Reptiles before Mammals, and so on. Plants show this exceedingly well. Lotsy (77) is of opinion that fossils do not prove phylogeny because all that they show is that one series follows another. He forgets to mention that this seriation is precisely the same as that of the natural system. Is it not a remarkable fact that in many cases the seriation of fossils in the successive geological strata is precisely that which would be expected from the systematic relationship of the classes, as deduced from their living representation?

But some critics point out quite rightly that the earliest Cambrian animals are among the most complicated of their class. This, for example, is true of the Crustacea. But such critics are making the mistake of confusing specific with class characters. If we compare the classes we find that the period in which Crustacea were most abundant is followed by the period in which Insecta are dominant although they themselves remain on in fewer and less complex form. The fact remains that the highest types of animals of the Ordovician and Cambrian were Invertebrates, Fishes of the Devonian and Silurian, Amphibians of the Carboniferous and Permian, Reptiles of the Mesozoic and Mammals of the Tertiary. Man is the last to appear and is the most differentiated if all his characters are considered. Among plants the same is true. The more highly differentiated fossil Pteridophytes never attained the complexity of our Orchids for example.

As one higher class succeeds another, so the higher members of the lower class may disappear, the lower ones remaining. It is from the latter alone, the more undifferentiated species of the older class, that the new class type can arise. These undifferentiated members survive to represent the ancestors of the new class. Lotsy, however, sees in these phenomena arguments in favour of his theory of hybridisation. The sudden appearance of numerous new forms of a class he compared with the result of a cross. Vertebrates, for example, arose by one crossing of two Invertebrates!

There is another fact from geology (or rather perhaps from astronomy) which justifies the belief that the simple forms preceded the more complicated. There are few facts so well established in the history of the earth as that the globe has undergone a process of cooling. Even on the planetesimal theory there must have been a time when life in its higher forms would be impossible. But *Cyanophyceae* and Bacteria can withstand temperatures markedly higher than those of many higher organisms, and it is in these groups that the representatives of the most primitive forms of life must be looked for, even if, as we have seen, some species classified with the Bacteria are in reality advanced.

VI. Taxonomic Characters.

Hitherto we have spoken of characters as if they were all of equal significance, and as if they were definite entities. These two suppositions are in apparent opposition to current views. It has long been known that in taxonomy some characters are of greater importance than others. If this were not so it would be impossible to build up a natural system on the method that has been adopted from the earliest times, namely, systematic categories subordinated to one another, as is the species to the genus, the genus to the family, and so on. Specific characters are distinguished from generic characters, and these in their turn from characters belonging to groups of more inclusive nature (family, order, class, etc.). A very little consideration of how this has been arrived at will show that the different and relative systematic values of characters in no way conflicts with the impartial treatment accorded to different kinds of characters in the previous sections of this work.

The most ancient systems of classification known, depended, as one would expect, on the most obvious characters. Aristotle and Theophrastus, for instance, grouped plants into trees, shrubs and herbs, much in the same way as one who had no knowledge of botany would probably do at the present day, if confronted with the necessity of

forming some kind of system. In the sixteenth century, when organised investigation of plants and animals was just beginning, similar schemes were in vogue. To take a botanical example; in Gerard's *Herball* (45) in 1597 trees and shrubs are still apparently regarded as primary groups, although herbs are divided into Grasses, Rushes, Corn, Flags, Bulbous Plants, Roses, Heaths, Mosses, Mushrooms and even Corals. As late as 1704, Ray (95) considered *Herbae* and *Arbores* as the two main divisions of the vegetable kingdom, although he discovered the importance of the cotyledons in classification. It was soon found, by observation of the plants themselves, that this mode of classification did not always bring together plants that were actually similar in the sum of their characters, and so other groupings were tried. At first it was thought possible to attain a satisfactory grouping by means of a single character which, it was hoped, would give a key to the whole organisation and thus bring organisms together that were really similar. On this idea of a key character depended several systems of classification that were put forward about the beginning of the seventeenth century, viz. those of Rivinus (97) and Tournefort (110) on the corolla, Camellus (14) on the fruit, Magnol (81) on the calyx and corolla and Linnaeus (71) on the stamens and carpels. This last system attained a great popularity on account of its great simplicity, and because it was associated with the binary system of nomenclature, and therefore the first clear ideas of genera and species. However, Linnaeus himself regarded his system as an artificial one, as is shown by his attempts to formulate a different system altogether. The latter was never completed, but in 1751 (72) Linnaeus published an arrangement of a number of genera which, as he stated, formed the fragments of a system. In these "Fragments" the genera are not arranged in orders by means of any key character, but on what he called the simple symmetry of all the parts. Linnaeus was followed by many other authors in his attempt to found a natural system.

It must be remembered that the natural system is an altogether pre-Darwinian idea, and largely originated from authors who believed in the independent creation of species. The main object was to bring together species which were similar in the bulk of their known characters.

The history of animal classification likewise begins with attempts to found systems of classification on one or a few characters, and finally arrives at systems in which all characters are considered. At the beginning of the modern period the chief characters used were taken from Aristotle's system. Thus, in 1552, E. Wotton (117) based his main

divisions on the presence or absence of red blood, and on the viviparous or oviparous mode of reproduction. He took into account the nature of the medium inhabited by the animal, and thus made the mistake which Aristotle had already avoided of placing Whales with Fishes. On the other hand, he added the *Zoophyta* to the bloodless animals, whilst the viviparous quadrupeds are divided into (i) many-toed, (ii) two-hoofed, and (iii) single-hoofed. Anatomical characters were first introduced into classification by J. Ray (1628–1705), and thenceforth played an important part. Linnaeus (73) used the number of loculi of the heart, the presence or absence of red blood, and the cold-blooded or warm-blooded characters as his most important distinctions. Vivipary and ovipary distinguish Mammals from Birds. The presence of lungs, as opposed to gills, marked off Amphibians, in which he included Reptiles, and to which he ascribed one auricle, from Fishes. In bloodless animals the presence of antennae distinguished Insects, and of tentacles Worms. A new class of characters was introduced into classification by Lamarck (66), for he describes Vertebrates as intelligent animals, whilst under the titles of sensitive animals and apathetic animals he divides Invertebrates into two groups, the former consisting of the Arthropods, Annelids and Molluscs, the latter of Nematodes, Tape-Worms, Tunicates, Echinoderms, Polyps and Infusoria. His use of psychological characters is not surprising in view of the emphasis he laid on use and disuse in evolution.

Until this time the system of animals had always been planned in the form of a linear series. Even Lamarck had not given up the old idea of a *scala naturae*. But with Cuvier (28), in spite of the fact that he was a strong opponent of evolution, the single series gave place to four main branches. He recognised that linear arrangements depend on the use of special characters rather than the general organisation. He found that the best indicators of the characters of the organism as a whole were the circulatory system and the nervous system, the variations in these two systems being especially closely correlated. The animal kingdom thus falls into four groups—*Radiata*, *Mollusca*, *Articulata*, *Vertebrata*. Von Baer (113) supported this fourfold division of the animal kingdom on grounds of symmetry; he called them respectively the peripheric, the massive, the longitudinal and the vertebrate types. He also took the important step of introducing embryonic characters. Numerous systems followed, based on detailed embryonic and anatomical characters as they were discovered owing to the activities in these departments of research. The use of the whole organisation was particularly emphasised

at a somewhat later date by R. Leuckart (69), H. Milne Edwards (83) and T. H. Huxley (62), forming the foundation of the modern systems.

The history of both botanical and zoological classification therefore shows that it is impossible to obtain satisfactory systems, *i.e.* systems which bring together organisms related by homological resemblance, on the basis of any one preconceived key character. At the same time, if all characters are considered in an impartial manner it is found that some are distributed through greater groups of animals than are others, and hence the fragments of truth contained in the old classifications into bloodless and blooded, into warm-blooded and cold-blooded, and into vertebrated and invertebrated animals were founded on the early recognition of the obvious fact that the main characters in any system of classification must be those having a wide distribution in the animal and plant kingdom. In fact it appears certain (98) that Aristotle was aware of the principle that affinities must be traced from a knowledge of all the characters of the organism. For the different taxonomic values, accorded to different characters, were of course, arrived at from observations on the distribution of characters among the various species of animals and plants. Some characters were found common to large groups of species, others confined to smaller aggregations. The larger groups included the smaller, and thus the characters common to the larger groups assumed a greater importance than those of the smaller. Each character, as it is observed in nature, must be accorded equal weight; there can be no evaluation of characters on the nature of the characters themselves. Only if their distribution in a number of different species is known can their relative value in classification be definitely ascertained. As it happens that individual variation is proportional to species variation, as Darwin long ago demonstrated (29), the distribution of a character in individuals may also be used in determining its systematic value.

There has therefore been no need in the earlier parts of this work to assume any difference in the value of characters, in fact any supposition would presuppose the results of comparing the distribution of characters.

In spite of the fact that the whole organisation of the plant or animal should, in a system which represents nature most completely, play a part in classification, a consideration of the number of characters that may be used, even in the simplest of organism, will show that such a system is impossible to attain. The system must in practice be based on a few characters. Are we therefore to revert to an artificial arrangement? A negative answer to this question seems possible if it is re-

membered that any system is based on a limited number of characters, and therefore is in a sense artificial. Excluding this conception of artificiality, which is inherent in all scientific description, it is possible to distinguish artificial and natural arrangements on the basis of the characters selected. For example, the placing of *Volvox* with the other colonial Chlamydomonads is natural as far as some characters, *e.g.* colony form, are concerned, but unnatural if we consider others, *e.g.* cell wall structure.

A very important change in our conception of the natural system is suggested by the recent work of B. Hayata (57) on the above basis. This author, in proposing a system of classification for the flowering plants, recognises the principle that a system should be subject to change according to the point of view taken in describing the species. He controverts the usually accepted idea that only one natural system of classification is possible. He speaks of his system as a dynamic one, because species, genera and families, can be moved about, not arbitrarily of course, but according to the characters considered at the moment. Some of these arrangements will obviously represent blood relationships more closely than others.

The consideration of characters as separate entities must now be justified. Every physiological fact tends to show that the parts of every organism are intimately dependent upon one another. Even independence in inheritance, as appears in Mendelian characters, or their factors, cannot be assumed to be associated with the majority of systematic characters. The use of the term character in the preceding sections depends on the fact that species and other systematic groups are distinguishable by differences which can be observed and measured. It is true that in taxonomy merely individual characters are excluded, but the characters used are not hypothetical physiological stimuli, or Mendelian factors. The differences dealt with in Mendelian experiments are really taxonomic differences of a special kind, *i.e.* those distinguishing varieties or species which are sufficiently closely related to be capable of interbreeding. The other characters used by taxonomists in discriminating species are in every way as definite as those used in Mendelian inheritance, although they may not depend on unit factors.

Whilst they may not depend on unit factors, Mendelism has dealt with the various ratios with which members of a given fraternity[1]

[1] It is unfortunate that the term *family*, which in its everyday sense would have been useful when groups of interbreeding individuals are studied, has become generally accepted in biology as the name for a systematic category above the genus.

exhibit their combinations of characters, and hence gives nearly exact quantitative data on this subject. The characters themselves have not usually been dealt with in a quantitative manner. Each character is thought of as a unit or more generally as the interaction of several units or genes, but the actual extent to which each gene affects the plant or animal as a whole is a problem in developmental mechanics which has hardly been tackled so far. Hence the Mendelian knows no more, and may know less, about the actual characters existing in species than the taxonomist does, although the former has contributed to a knowledge of the way in which characters combine in individuals. The taxonomist moreover has the advantage in dealing with the characters of larger groups than species, whereas the Mendelian has to content himself with groups of organisms capable of interbreeding.

The treatment of species by reference to a number of separate characters may be thought to be an artificial process, based on convenience. But in this respect it does not differ from any other method by which one set of facts is abstracted from its relations. The species in taxonomy is only a relative term. But although not absolutely distinct from another the characters of the species, like the species in the system, are to some extent independent. The organism is not a homogeneous mass of protoplasm and the characters into which we divide it are generally suggested by the structure of the organism itself. Meristic characters are certainly of this nature and can easily be measured.

VII. Mendelism and Phylogeny.

In the course of evolution a number of inherited variations must have come about, giving rise to the different types characterising the various phyla, classes, orders, families, genera and species. The variations used in Mendelian experiments are inherited, and of recent years have been considered as identical with the variations concerned in the origin of the natural system. The reasons for this appear to have been as follows. In the first place Mendelian experiments were largely made with cultivated races of animals and plants. Since Darwin's comparison of artificial with natural selection (29), there has always been a tendency to regard the origin of cultivated races as a model of evolutionary processes in general. Thus De Vries (33), and especially Korchinsky (65), found evidence for mutation amongst cultivated plants, Lotsy (76) for evolution by means of hybridisation from practically all cultivated plants and animals. Morgan's more recent views on mutation as a method of

evolution (87) are founded on observation of mutants arising in artificial cultures, and therefore have a similar foundation. Most authors believe that there is a close analogy between the origin of cultivated races and the origin of species in nature. If this is so then the variations in character studied in the very numerous Mendelian experiments that have been carried out on cultivated races may serve as a model for the variations in the characters of species occurring in nature, and hence for the changes concerned in phylogenesis. And there is other evidence that this is so.

From the majority of cases where the cytology of the germ cells has been investigated, and particularly from the studies of T. H. Morgan and his school on *Drosophila*, the chromosomal mechanism appears as the necessary basis for the principles of heredity discovered by Mendelian experiments, as first suggested by W. S. Sutton (107) in 1902. But as Morgan (87) points out, the acceptance of the chromosome theory of heredity implies "a point rarely appreciated, namely, that the acceptance of this mechanism at once leads to the logical conclusion that Mendel's discovery applies not only to hybrids, but also to normal processes that are taking place at all times in all animals and plants, whether hybrids or not." If this is so, then all characters (except in organisms where chromosomes do not occur) are of the Mendelian kind, and must be regarded as due to determiners or factors in the chromosomes.

Opinion is divided as to whether this latter statement is correct. Even Morgan (87) admits that some forms of inheritance are due to bodies, other than chromosomes, residing in the cytoplasm. Boveri (12) appears to have believed that individual and species characters were determined by the chromosomes, but that those of higher systematic units had their seat in the cytoplasm. J. Loeb (74) likewise thought that the higher group characters were dependent only upon the cytoplasm. J. P. Lotsy (78) has recently expressed a similar view. R. R. Gates (42), after making an extensive survey of characters of all kinds in animals and plants comes to the conclusion that they are of two main kinds, organismal characters and karyogenetic ones, the latter alone being dependent on the chromosomes. It would appear that both kinds have various systematic values. Other recent authors will not admit that mutation has played any part in evolution. E. W. MacBride (80) points out that the best authenticated cases of mutants, such as those obtained by Morgan in *Drosophila*, are all abnormalities, which are distinguished by characters totally unlike those differentiating species. The *Œnothera* mutants of De Vries (33) are now generally considered as hybrids of a peculiar nature (77).

If the chromosomes have the importance which the Mendelians ascribe to them, the nuclear characters should be veritable key characters. Unfortunately only the grossest features of the chromosomes are visible under present microscopic methods; differences which may be of the highest genetical importance remain quite invisible. It is not surprising then that attempts to correlate chromosome equipment with the general systematic characters have not met with conspicuous success. Nevertheless it is impossible to deny that some kind of relationship may exist. The Protozoa as a whole show much simpler nuclear structure than the Metazoa and Metaphyta, nevertheless the main types of protozoal nucleus, as summarised by Calkins (15) and Minchin (84) for instance, do not appear to correspond to special groups. But much care is needed in drawing negative conclusions. The Algae show almost as much variety as the Protozoa in their nuclear structure, but H. v. Neuenstein (88), from a detailed study of all groups, except *Cyanophyceae*, concludes that a general relationship exists between nuclear structure and systematic position. And the *Cyanophyceae*, which undoubtedly have a peculiar cytological structure, are marked off from all other Algae by a number of peculiarities (26), and thus form a very distinct group. The nuclei of Fungi are amitotic or show few chromosomes. The *Hepaticae* show low chromosome numbers in general; certain Pteridophyta are characterised by high numbers. Occasionally a plant group may have a characteristic chromosome number, or more frequently a characteristic grouping (16). Amongst animals McClung's (82) work on the *Orthoptera* seems to be the most convincing example of the same kind.

Another recent development in taxonomy is the attempt that has been made by certain authorities to interpret the relationships of related species in terms of unit differences. Sturtevant (106) examined species of *Drosophila* with a view to comparing them with the mutants obtained in culture. Bateson (2) applied Mendelian conceptions to the specific differences in certain genera of Birds, and Gates (41) and Small (104) have treated genera and families of plants in this way. There does not seem to be any opposition to the phylogenetic method in this procedure, in fact both Gates and Small have given phylogenetic tables of groups dealt with in this way, and it is noteworthy that in the case of *Drosophila*, the only case in which there is abundant evidence for the existence of unit factors, the experimental mutants differ strikingly in a few characters, whilst the natural species differ from one another in innumerable characters. And, as MacBride (80) has pointed out, Sturtevant only finds suggestions of similarity between mutants and species, "and to do this

he has to search amongst different genera, sub-families, and even sub-orders." MacBride gives an example of a Crustacean genus (*Gammarus*) in which mutants are known with defective eyes and in which also natural species occur with defective eyes. The mutants are known to behave in a Mendelian manner when crossed with the type, but the histology of the defective eyes of the mutants was of a nature totally different from that of the natural species and their allies which have reduced eyes. And the Mendelian characters distinguishing the different varieties of cultivated plants and animals, which form the bulk of the material on which Mendelian investigations have been carried out, are not generally characters that could have persisted apart from the interference of Man, who has substituted an artificial selection which differs in direction from that of natural selection. The numerous forms eliminated in nature are, however, equally expressive of the potentialities of the species to evolve, as are the comparatively few that survive, and are therefore spoken of as natural; and the possiblity that some species arose as mutants cannot be overlooked.

If a series of species have originated from one another or from a common ancestral form by mutation, does this affect the possibility of tracing their phylogeny? Suppose a mutation to take place. This mutation may then in some cases be of such a nature as to render the new form better fitted to its environment than the parent form and by the action of natural selection the balance of number of individuals, which at the time of the birth of the mutant was infinitely in favour of the parent form, is now such that the new form at least competes to some extent with the parent.

In other words, suppose the mutant form is able to reproduce abundantly. Let $1 : x$ be the proportion of individuals of the mutant type appearing in a given population of the species during a given time. If the mutant form is able to reproduce to the extent of giving rise to a total of x individuals, then amongst them one further mutant may be expected if the rate of mutation is the same in the mutant form as in the original parent type.

And it would be possible to arrange the successive mutants in a phylogenetic series. Suppose a combination of characters $A\,B\,C\,D$ to give rise to a combination $A'\,B\,C\,D$, and this in its turn, after considerable reproduction, to give rise to a further combination $A'\,B'\,C\,D$ and so on, then if all the forms persist they can be arranged in one definite phylogenetic series and one only, viz.:

$$A\,B\,C\,D, \quad A'\,B\,C\,D, \quad A'\,B'\,C\,D, \quad \text{etc.}$$

But it has been assumed by some authors that if mutations take part in evolution then, inasmuch as they come into the process, it is impossible to formulate a phylogenetic series. This would follow from the conclusions arrived at by Duerden (36) in his consideration of a number of diverse morphological facts from the Mendelian point of view, and they must therefore be considered in some detail, as illustrating the incidence of the Mendelian hypothesis on phylogeny. Apart from the criticism of Tate Regan (96) that Mendelism is a theory of heredity, not of evolution, that embryological evidence points to gradual change, and that change of habit precedes change of structure, there are, on the basis of what we have already concluded with regard to mutation, reasons for interpreting the examples given by Duerden in a different manner and as quite in harmony with phyletic concepts.

The author first deals with origin of feathers from scales in the Ostrich. On the leg of the Ostrich at the time of hatching, there is a transition from scales, rudimentary feathers growing out of the scales in the intermediate region between scales and feathers. There is here obviously a relation between feather and scale, although, as the author points out, the condition in the Ostrich chick may not represent the original relationship. Duerden considers that this relationship can be interpreted by two different methods.

(i) The older method of comparative morphology: that it represents, to some extent, the course of evolution from the reptilian scale to the avian feather. The former "has grown upwards into a filament, and by a complicated system of incisions of the epidermis, due to ingrowths of the dermis, the filament has become frayed out, and given rise to the many structural divisions of the feather-shaft, barbs, and barbules." The author points out that this has largely been accepted, and that the parts of the feather can be homologised with corresponding parts of scales, claws, nails and hoofs.

(ii) The second interpretation, called by Duerden Mendelian, is that the feather is an organ *sui generis*, dependent on a separate germinal change, its position on the scale being merely incidental. The corresponding parts of scales and claws, nails and hoofs all depend on separate factors and "to establish a correspondence of parts does not imply a unity of origin." The author thinks that the same argument can be applied to cases of homology, and that "the tracing of a corresponding structure through all its many transitional stages, from one extreme to the other, is but a delusion if a genetic relationship is the underlying idea."

This second interpretation of Duerden is not based on breeding experiments, and the assumption that the difference between scales and feathers depends upon a Mendelian factor or factors is unwarranted. No one has yet crossed a Reptile with a Bird and obtained Mendelian results. But even admitting an analogy between the difference in question and Mendelian differences it must be remembered that the latter are necessarily differences between characters that are homologous. Although allelomorphic characters may differ considerably they do not differ in morphological nature. Thus *yellow flowers* may be allelomorphs to *white flowers* but not to *mottled leaf*. The organisms taking part in the cross must consist of equivalent parts, otherwise the cross will not occur. This is why it is not possible to hybridise unrelated organisms and probably accounts for the fact that many hybrids are sterile.

If the chromosome mechanism be considered it will be realised that the nuclear contribution of each parent in a fertile cross consists of equivalent parts. On the chromosome theory of heredity each organ is represented doubly by similar genes in the diploid phase, except the organ affected by the cross. In the case of this organ there are two different genes and if one dominates the other, this, and not its fellow, will determine the character of the organ. In blends both members of the pair of genes come into play. But both members of the pair are thought to occupy the same relative position on the homologous chromosomes, and they have a reciprocal action on the organism.

Certain other cases cited by Duerden also have a direct bearing on the reconstruction of phylogeny and may be cited here, with the object of showing that Mendelian interpretations of systematic series do not make it impossible to establish a phyletic relationship amongst members of the series. The Lizard genus *Chamaesaura* consists of three species all living under similar conditions in South Africa, all showing reduction in limbs and increase in the tail as compared with other members of the order. The characters of these species we may summarise from Duerden's description as follows:

Species	Length of fore-limb in mm.	Length of hind-limb in mm.	No. of digits	
			Fore-limb	Hind-limb
C. oenea	9 to 11	14 to 16	5	5
C. anguina	6	8	2 (small)	1 or 2 (small)
C. macrolepis	0	6 to 7	0	1

This is obviously a reduction series and on the assumption that the system of classification represents the course of evolution, no difficulty whatever would present itself in arranging these species in a definite

sequence, *C. oenea* representing the oldest and so on. But Duerden adds an alternative interpretation based on the Mendelian point of view. He says: "Each would represent a distinct phase of degenerate evolution, wholly unconnected with the two others; *anguina* need not have passed through an *oenea* stage, nor *macrolepis* have descended from *anguina*."

Now it seems in the highest degree unlikely, even on a full acceptance of a chromosomal basis for the characters, for which there is not the slightest experimental or cytological evidence in this case, that the changes resulting in the three species are due to independent factors. For this would imply in the case of the hind-limb the existence of one factor, the absence of which in *C. anguina* would give a hind-limb of 8 mm., another factor, the absence of which in *C. macrolepis* would give a hind-limb of 6–7 mm. But from the cases of stature inheritance known in Vertebrates such an explanation would be exceedingly unlikely. It is true that analogous differences have been the subject of Mendelian experiments, but in all these the explanation of the progressive difference is that of additional or cumulative factors.

If a Mendelian explanation of the difference between the three species of *Chamaesaura* is supposed, then it is infinitely more probable that *C. macrolepis* originated from forms like *C. anguina* by loss of one or successive loss of more than one factor, than from forms like *C. oenea*, or still more from a typical lizard, by the loss of one, or the simultaneous loss of a large number of factors.

In general terms the series of species which differ from one another by characters dependent on the chromosomal mechanism can be expressed as a series, each member of which is dependent on a number of factors which are independently variable. Let these factors in any given case be expressed thus:

$$A\,B\,C\,D.$$

Then other members of the series can be expressed:

$$A'\,B\,C\,D,\quad A\,B'\,C\,D,\quad A'\,B'\,C\,D.$$

But if the chances of the mutation from $A\,B\,C\,D$ to $A'\,B\,C\,D$ are represented by $1 : x$ then the chances of the mutation from $A\,B\,C\,D$ to $A'\,B'\,C\,D$ occurring are $1 : x^2$. Now mutations, as already pointed out by MacBride (80), are very rare and x is certainly greater than 1000. Therefore it is almost certain that if organisms of factorial composition $A'\,B'\,C\,D$ actually exist then they have arisen in two steps:

$$\alpha \begin{cases} (1) & A\,B\,C\,D & A'\,B\,C\,D \\ (2) & A'\,B\,C\,D & A'\,B'\,C\,D \end{cases}$$

$$\text{or } \beta \begin{cases} (1) & A\,B\,C\,D & A\,B'\,C\,D \\ (2) & A\,B'\,C\,D & A'\,B'\,C\,D \end{cases}$$

And in the cases cited by Duerden $A = B$ so that the alternatives α and β do not differ. The two steps can in such a case be arranged in one phyletic series; if α is unlike β then there are two possible phyletic series.

It is clear then that if specific characters depend on unit chromosome or other independent factors as they have been supposed to do in some series then, far from making phylogeny an impossibility, they considerably lighten the burden of the investigator attempting to classify the group, inasmuch as they give to the species a definiteness which it would not otherwise possess, and which certainly does not exist in a large number of groups, as has already been shown.

Another aspect of the influence of Mendelian ideas upon phylogeny is seen in the interesting and important criticisms of J. P. Lotsy. After writing an extensive work on the phylogenetic history of plants (76), Lotsy turned his attention to the method of evolution and came to the conclusion that hybridisation was the important factor (77). In this later work he expressed the view that his theory of evolution was destructive of his own earlier attempts to trace the phylogeny of the vegetable kingdom. He says: "Phylogeny...reconstruction of what has happened in the past, is no science but a product of phantastic speculations, which can be held but little in check by the geological record on account of the incompleteness of the latter." Still more recently, however, he has again modified his views (78), and now believes that the phylogeny of the gametes can be traced, although with difficulty, owing to a base unaffected by crossing in the cytoplasm of the cell.

Lotsy (77) crossed certain species of *Antirrhinum* and found that the offspring were of numerous new types. The deviation of the offspring from the parents and amongst one another was in some cases so great that the various types might have been placed in different genera. He shows that hybridisation is very abundant in nature, and largely accounts for the diversity of forms in higher plants, insects and other large groups. It will be unnecessary to discuss his attempt to prove the origin of the great groups by hybridisation (77), since he appears to have modified his views on this aspect of the subject (78). He shows, however, that some species may arise by crossing and may hence have a polyphyletic origin. At the same time, specifically and generically distinct

forms may be produced within a single fraternity. Consequently he thinks phylogeny is untraceable, at least as far as species are concerned. His conclusions will be considered in the next section.

VIII. Individuals and Species.

Anatomy, embryology and taxonomy are sciences in which the unit of study is a group of individuals. In human anatomy, for example, the characters common to all individuals are the centre of interest, yet it is clearly recognised that no two individuals are alike. It is impossible, however, to take into account every individual variation, so the latter must be studied by statistical methods, or a few special individuals selected for study. Comparative anatomy and taxonomy are often concerned with the characters of larger groups. Thus in discussing the morphology of Birds and comparing them with Reptiles the comparison is based on class characters, *i.e.* characters common to the majority of Birds or Reptiles. The avian type is therefore compared with the reptilian type, but not any single species of one class with the other, still less any particular individuals. In such a comparison the characters differentiating the different species of Birds or of Reptiles amongst themselves are of no concern. These latter characters, inasmuch as they can be separated from class characters, throw no light whatever upon the relationship between the classes. In embryology too the unit is a group; groups smaller than the species are seldom described, and it would be quite impossible to enumerate the vast number of minute variations in ontogenesis which must differentiate between the individuals of any one species.

In studying phylogeny, as in ordinary embryological studies, individuals are not dealt with. The attempt is made to trace the descent of species, genera or other groups, but not of individuals. It is of course possible in human individuals to trace the individual ancestors in a number of particularly favourable cases. And the same is true of some of the particularly favoured individuals amongst our domestic and experimental animals and plants. The tracing of individual descent is the task of genealogy, which is a biological science in embryo, but which, with the results of Mendelism which properly belong to it, may develop in the future. Genealogy has hitherto been confounded with phylogeny, owing to the close analogy of individual with group descent. But a little consideration will show that its aims and methods are totally distinct.

The tracing of individual descent must be limited to a very small number of generations, otherwise the work quickly assumes prodigious

dimensions. Each human being has 2^2, 2^3 ... 2^n ancestors in n generations. So if fifty-six generations are assumed to have elapsed since the beginning of the Christian era each living individual can claim since that time 139,235,017,489,534,976 ancestors, some of which are identical, but all of which should appear in a genealogical table. And this period represents the merest fraction of the history of the genus *Homo*.

Phylogeny deals with the origin and succession of characters, not with their distribution amongst individuals. Species, genera and other groups are mere aggregates of characters not having a physical existence, but none the less the logical outcome of facts. By a consideration of all the characters of any one of these groups, its systematic position can be definitely established, and the phylogeny is represented by this position as has already been shown.

Lotsy (78) believes that the genealogy of gametes can be traced. But what does the gamete mean in the Mendelian sense? Obviously not merely a single cell, or maybe a single nucleus, as in the egg of flowering plants or sperm of animals. From the Mendelian point of view the gamete is thought of as much more than this, as the bearer of the hereditary qualities, in fact as a vast collection of potential characters. Hence genealogy of the gamete means phylogeny of characters, and this is precisely the way in which phylogeny was conceived and is still used by morphologists.

As phylogeny is not genealogy, it does not affect phylogenetic conclusions if distinct generic characters are found together in the offspring of a single cross. Crosses, however wide, occur between organisms that have homologous parts, and however much the offspring differ they can be arranged in order according to the degree of development of their homologous characters. And this order represents the phylogeny, *i.e.* the order in which those characters arose in the course of evolution. Of course a character may remain latent through a large number of individuals and then reappear, but this has nothing whatever to do with its phylogeny.

Any combination of characters, forming a species, may, it is true, arise by crossing, and that combination may disappear and reappear any number of times. But apart from the history of the individuals in which this combination is manifested, the combination itself has a systematic position, based on a comparison with other combinations of characters. It will not be easy in all cases to arrive at the systematic position. The natural system cannot be represented by a two-dimensional coordinate system. There will be as many dimensions as characters.

But as the species has not, like the individual, an absolutely infinite number of characters, there is a possibility of arriving at a definite conclusion. Particularly is this so with the higher groups, like classes, which are abstractions of fewer and fewer characters[1].

The precaution against confusing characters belonging to different systematic categories was made clear by Cope (19), who says: "If, for instance, it is alleged that such a genus is ancestral to another genus, it is often forgotten that the descent of generic character, and not specific character is meant." He points out that attempts to contradict such an hypothesis of generic descent by reference to some incongruity in specific character are irrelevant. For example, although *Hippotherium mediterraneum* cannot be the ancestor of *Equus caballus* this is no proof that the genus *Hippotherium* is not ancestral to the genus *Equus*. For there are many other species of both genera. Cope also remarks that the condylarthrous Mammalia are ancestral to the *Diplarthra* is not disproved by the fact that "no known genus of the former fits exactly the position of ancestor to any genus of the latter, in the present state of knowledge." The principle appears sufficiently important to receive a special name, and I propose that it should be called Cope's Law.

But if this principle is admitted it should be applied to the species as well as to the genus, family, order and class. And hence criticisms of phylogeny of species on the basis of the descent of individual characters cannot be accepted as legitimate. Unfortunately Cope's Law has been little recognised in dealing with the higher categories and certainly has been persistently neglected with regard to species.

A second principle may be added, viz. that the distribution of specific characters amongst individuals does not affect the facts of seriation of these characters amongst themselves. And the same applies to generic and higher group characters. The seriation of the characters is not even necessarily identical with[2] the order of their first appearance in time, although no doubt it generally is, as shown by the facts of palaeontology.

[1] Recently attempts have been made, especially by palaeontologists to define the great groups by evolutionary tendencies rather than by definite characters; see F. A. Bather (3). But such tendencies are themselves recognised by the presence of some common element throughout the series in which the tendency is exhibited even if this element be of a highly abstract nature.

[2] It always *represents* this order but may not always be identical. The direction of evolution in a particular group may not be known and the phylogeny put forward in such a case may be the reverse of the actual order of appearance. It nevertheless represents the actual, much in the same way as an inverted image in a concave mirror represents an object. Analogous cases will suggest themselves to the reader.

The natural system, and hence phylogeny, is complicated by the fact that different characters may give different indications of affinity in one and the same organism. Every morphologist knows that a type may be primitive in some respects and advanced in others. Man himself, so advanced in the sum of his characters, is very primitive in some features. Elliot Smith (105) has clearly indicated this, and illustrates it by the fact that, in his hands, Man retains more primitive characters than his nearest simian relatives. In general the highest differentiation has been attained by those animals which have kept a residuum of undeveloped features. I cannot, however, agree with Lotsy (77) that the Cow is more advanced than Man, even in the one character he selects for comparison, viz. the protective mechanism against wet feet!

The existence of some unspecialised organs in most animals and plants is only to be expected if evolution is a reality, unless most species have come to an end of their possible developments. It is from the unspecialised, primitive parts that future organs can best be evolved. And the fact that different characters may sometimes give conflicting phyletic conclusions must not obscure the other and more obvious fact, that the systematic position as based upon one character is generally confirmed by many others.

IX. Phylogeny as Theory and Hypothesis.

The study of race development, unlike that of individual development, will always be largely a matter of theory and hypothesis. Apart from the fascination which the subject has for many minds, which in itself may seem a sufficient justification for its pursuit, there are reasons for regarding the formation of clear theories and sound hypotheses on this and other scientific questions as something more than the development of mere *memoria technica* or artificial aids in fitting facts together. Many authors could be cited who rebel against the logical and speculative aspects of science in general, and who consider observation as giving knowledge of a more certain kind than that gained by inference. This view has been set forth, for example, in a recent work by E. W. Hobson (61). Many other instances might be mentioned. But to prove that theories and hypotheses are of an entirely different nature to observations is not to prove them to possess a lesser degree of certainty than the latter.

Natural science, as opposed to mathematics, starts with perceived fact. The perceptions may be doubted but, if they have any degree of certainty at all, then, when we pass from percept to concept by a process of logic we must be equally certain of our concepts, provided we have

made no mistake in our logic. I am here referring to what Hobson calls immediate concepts, and what most people call natural laws, as distinguished from hypotheses. Further, the certainty of these laws, in those cases where they refer to material objects, may be verified by any number of actual experiments. In other words, having once made a concept, we can pass from concept to percept again. The concept is never the same thing as the percept, but it bears a definite relation to it and has the same degree of certainty.

Hypotheses, unlike theories, involve something more than pure logic. In their formation the imaginative faculty undeniably comes into play. Hence it is not improper to trace an element of phantasy in their construction. But phantasies are of many kinds, and some sorts of phantasies lead to the discovery of the objective fact. If hypotheses were incapable of leading the mind from percept to percept, invention in every form would be impossible. All sorts of hypotheses can be made, by the aid of phantasy, about a given set of facts. All of these are equally removed from physical reality, but some will stand the test of physical reality when it comes to new experiments or fresh observations. Hypotheses further lead to the discovery of new classes of physical facts, and thus differ from natural laws which only state what is already known.

In the last resort it can only be said that logical thought, as opposed to illogical thought, depends on some peculiarity in the psychological mechanism of the thinker which leads him to what we call a correct, rather than an incorrect judgment. Phantasy thinking, like logical thinking, may also sometimes prove fertile, as in the case of the inventor or the discoverer, although why in some cases and not in others can only be ascribed to a difference in the psychological mechanism of the individual. The inventor or discoverer resembles the artist inasmuch as he depends to some extent on his imagination. But in the former case it may be said with confidence that the statement "it is no use arguing about taste" does not apply, since in his success as an inventor we have a reliable test of the quality of his taste in hypotheses.

Phyletic hypotheses may not so frequently be put to test as those of many other branches of science, since experiments cannot be made. But many instances of phyletic hypotheses, which have received verification or still more frequently additional support since they were enunciated, might be cited. For example, the early hypothesis of the correspondence of the skull of Man with that of other Vertebrates, which may now be said to have become a theory, led Goethe to the discovery of the human intermaxillaries. The fact that phylogenies, subsequently

discounted by the discovery of new facts have been proposed in the history of the subject, does not prove the impossibility of arriving at truth. For since the conclusions of phylogeny are not readily checked, it naturally lends itself to loose speculation. And until authors have learned that at least as much, and probably much more, care is needed in phylogenetic conclusions than in making their preliminary observations, little further progress can be expected.

From what has been said with regard to hypothesis, it follows that little attention need be paid to the criticisms of H. Driesch (35), who, following Du Bois Reymond, compares the study of phylogeny with the tracing of the genealogy of the gods in mythology. It is true that he has seized upon an essential similarity between phylogenetic hypothesis and myth in that they are both partly the work of the imagination. But Driesch makes no attempt to work out the comparison. Yet many hypotheses of science may have their roots in ancient methods of thought. Driesch's own conception of entelechy could easily be traced to ideas of a very primitive order. Evolution and energy are concepts that have retained their identity, although no doubt profoundly modified, from the earliest times. The Mendelian theory, as has been suggested by C. G. Jung (64), may be derived from a myth of widespread occurrence. Is it then unlikely that some sort of connection might be traced between phylogenetic hypotheses and earlier forms of thought?

But on making such a comparison, it is clear that although phylogeny has itself had a history and may not have arisen by mutation, yet it is far from having any close relationship with myth at the present time. And in the future is it not likely that it will develop farther and farther away from its mythic ancestry?

Perhaps one criticism of theoretical biology that may be made, is that it is not possible to obtain absolute definiteness. In the physical sciences, mathematical methods may be employed, and an appearance of absolute definiteness is obtained. But it must be remembered that in these sciences the mathematical formulae only represent the facts, they are not the facts themselves. The perceived phenomena of physical science always differ from the calculated, although closer and closer approximations are continually being made. And mathematical methods are being more and more frequently applied to problems of evolution with increasing success. The aversion with which many biologists view attempts to describe evolutionary processes in mathematical terms, lies in the recognition of the fact that the problem is largely a historical one, and hence mathematical expressions of it, such as are used in

physical processes, can represent only a very incomplete view of the facts.

No doubt every function of the organism, including its evolution, is explicable by physico-chemical laws. The recent work of D'Arcy Thompson (109) shows how much, even now, can be said of the energy changes which determine growth and form. But such a work is certain to represent a distorted or at most a one-sided view of the structure and development of organisms unless a historical background is added. To take one instance. Thompson shows us how the "membrane" or "wing" of certain Flagellates is nothing more than a physical effect of the consistency of the protoplasm and the peculiar position of the flagellum. But he does not tell us how it comes about that in this particular species these special physico-chemical conditions are met with, whilst in another totally different conditions are found. And even if organic differentiation and heredity in general be explained, as no doubt they will be, then these explanations must still be supplemented with theories or hypotheses describing the origin and course of evolution of each particular species or other group, just in the same way that to account for any particular embryonic change in the life history of an individual by these general laws of heredity and differentiation is to give a stone where bread is asked for.

In face of the arguments set forth in the preceding sections, I believe it is absolutely impossible to maintain that the phylogenetic conclusions from classification are worthless. I think it has been shown that they have a definite meaning, and have endeavoured to point out what that meaning is. The relationships of organisms with one another are not theoretical interpretations at all, but descriptions of the actual facts of the relationships of parts of one organism to another. Phylogeny consists of theories and hypotheses formed from these facts. It is true that similarity is not the same as relationship, and that the organisms must have homologous parts. But even this can generally be settled by careful observation. Because in a few cases we are doubtful as to whether a resemblance is a homology or an analogy, that does not invalidate the infinite number of cases where there is no doubt. The leaf of flowering plants is undoubtedly homologous through the group, but may or may not be homologous with that of Lycopods. Or take the vertebrate backbone. Because there are a few species of Chordata in which the backbone is badly developed or absent, is this to cast doubt on the homology of the column throughout the great majority of the vertebrate series? Such a doubt would be a preposterous hallucination. Yet

such a fear seems to be present in the minds of some writers. W. H. Lang (68) uses the words "to abandon phylogeny as the only real basis of morphological study." But has phylogeny ever been the basis of morphological study? On the contrary the reverse is true. Phyletic conclusions have been the aim of much morphological investigation, and are the sum of the results obtained from the most difficult part of it, namely, the synthesis of a very large number of comparisons. Morphological data themselves give rise to the idea of some sort of relationship, and it was largely from this idea of relationship that the doctrine of evolution originated.

The problem of the cause of convergence and parallel development is of course an extremely important one. But inasmuch as convergence itself was discovered by systematic and morphological investigations, and is itself a phylogenetic conclusion from the systematic and anatomical facts, the necessity of making more detailed study of phylogeny is all the more necessary. Phylogeny will become all the more essential to the proper understanding of biological problems. To use the polyphyletic origin of a group formerly supposed to be a natural (monophyletic) one as an argument against the possibility of constructing a natural system is nothing more nor less than to use the conclusions of phylogeny to disprove phylogeny.

It is unnecessary to pause here to consider whether phylogeny is a descriptive or an explanatory science. For all science is descriptive in some respects. Phylogeny is a descriptive science in the sense that it describes relationships, it is that branch of morphology which deals with the similarities of structure that can be homologised. The study of morphology deals with structure in its widest sense, and is based on anatomical and systematic descriptions. Phylogeny therefore is the most difficult of the morphological sciences, and can only be attacked by students who have a thorough knowledge of anatomical and systematic facts. Few of us can pose as authorities on such a subject, but we can at least understand the methods on which it is based.

It is true that an identical type may possibly originate more than once in time, but phylogeny is not genealogy. It is a historical science but is not the history of individuals. The systematic group is its unit and with the origination of the members within the group it is not concerned. The origin of the same type more than once from the same ancestors is not polyphyletism as ordinarily understood, and cannot be made an excuse for the acceptance of polyphyletic groups in the natural system.

The natural system is an ever changing one. Groups found to be monophyletic are discovered to be polyphyletic. Botanists still tolerate artificial groups such as *Sympetalae*, and the even more ridiculous one of the Lichens. Zoologists have freed themselves from Worms, but they are still subject to Sporozoa. The reason for this is found in the inconvenience of continual changes, in museums, herbaria and systematic treatises. But why should we not adopt a purely artificial arrangement for such purposes? As a matter of fact most museums are not arranged on a natural system. Let this frankly be admitted; but let us continue the quest for a purely natural system of groups, a quest that must long continue in view of the infinite variety of organisms and the extreme complexity of their forms.

X. Conclusion.

It has been generally agreed within recent years that the older type of speculative phylogeny has proved ineffectual. This has led to a tendency to abandon the phylogenetic method, with a consequent one-sided interpretation of structure, as in the so-called Causal Morphology. To remedy this lack of balance an analysis of the true capabilities of the phylogenetic method became necessary and this is what has been attempted in the foregoing work. It was suggested by great difficulties which arise when an attempt is made to trace the phylogeny of lower types of organisms, viz. those with relatively few characters.

The main conclusions which have been arrived at may be briefly tabulated:

(1) That the construction of phylogeny is not an arbitrary matter but depends on certain facts concerning the natural system.

(2) Phylogeny consists of theories and hypotheses which do not differ in their nature from those of other branches of science. A satisfactory theory of the phylogeny of a group must however state the characters on which it is based.

(3) Convergence, which has hitherto been urged as one of the greatest objections to phylogeny, is a result of phylogeny and cannot be upheld as an objection to the phylogenetic method.

(4) Regression, although probably undetected in many cases, is likewise not a real obstacle to phylogenetic research.

(5) Mendelism and consequent possibilities, even if accepted, do not affect phylogenetic conclusions.

(6) The confusion of phylogeny with genealogy and the consequent misinterpretation of the aims of phylogeny has led to objections to the

phylogenetic method which are without foundation. Cope's Law must be applied to individuals as well as to groups, as has not hitherto been recognised. Thus in tracing the phylogeny of species no account should be taken of the descent of individuals (genealogy) within the species any more than, according to Cope, one should take account of purely specific characters in tracing the descent of genera. The effects of this are far reaching and should be studied in connection with the section on Mendelism. A consistent system of phylogeny can be built up if this principle is recognised.

(7) The comparison of phylogeny with earlier forms of thought cannot in any way be regarded as an objection to it. Similar comparisons can be applied to any branch of scientific thought.

In conclusion the writer must add that he is fully aware that much further investigation of the principles of phylogeny and, in fact, of morphology in general are necessary. He can only hope that he may stimulate more experienced biologists and philosophers to investigate the subject. For his boldness in attempting to take the matter up he can only plead the perennial interest of the problems of organic descent.

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LINKAGE PHENOMENA IN WHEAT.

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(With Four Plates and Fourteen Text-figures.)

CONTENTS.

INTRODUCTION.

IN 1914 (11) my attention was drawn to the phenomena of linkage in wheat. At that time I expressed the supposition that the factor producing the long ears of *Triticum Spelta* is coupled with that producing the shapes of glumes and spikelets characteristic of this species of wheat.

The shape of the glumes of *Tr. Spelta* I considered, at that time, to be a single Mendelian character. *Tr. Spelta* crossed with *Tr. vulgare* gives in F_1 generation intermediate individuals, and in F_2 appears a segregation into three types, namely *Tr. Spelta*, intermediates, and *Tr. vulgare* in the proportion of 1 : 2 : 1.

My observations were confirmed in 1923 by B. Kajanus (9). This author supposes, however, that the shapes of glumes and spikelets, and with them also the characteristic length of ears of *Tr. Spelta*, are caused by the presence of one Mendelian factor only. My later investigations have shown that the shapes and sizes of glumes and spikelets do not constitute, by any means, a simple Mendelian character. In 1918 (12) I suggested that the shapes and sizes of the glumes of *Tr. vulgare*, *Tr. dicoccum* and *Tr. Spelta* are determined by numerous Mendelian factors. This conclusion was based upon the results of crossing *Tr. vulgare* with *Tr. dicoccum*. In F_2 from this cross numerous new types have appeared, and among them *Tr. Spelta* and *Tr. durum*. In 1912 (13) I suggested that in the cross *Tr. vulgare* × *Tr. Spelta* the factors producing the shapes and sizes of glumes and spikelets are linked in these two species. At the same time I believed that the phenomenon of crossing-over occurs in the F_1 of the cross *Tr. vulgare* × *Tr. dicoccum*, and that the aggregate of

numerous factors, mentioned above, breaks up in this cross. It seemed probable to me that by means of Morgan's theory of linkage and crossing-over these phenomena could be explained.

However, when I tried to bring all the observed phenomena into line with Morgan's theory, I noticed various difficulties.

Some of those difficulties were:

(1) I could not explain why the supposed phenomenon of crossing-over might be supposed to occur in the cross *vulgare* × *dicoccum* and yet did not appear in the crosses *vulgare* × *Spelta* or *dicoccum* × *polonicum*.

(2) I could not explain why the individuals of one of the parental types are more numerous in the crosses *polonicum* × *vulgare*, *dicoccum* × *vulgare*, *polonicum* × *Spelta* than the individuals of the other ones. In the three crosses, mentioned above, the F_2 individuals reproducing the types *polonicum* and *dicoccum* were more numerous than those representing the types *vulgare* and *Spelta*.

(3) I could not explain why the individuals reproducing the parental types in the crosses between tetraploid and hexaploid species appeared in such small numbers as compared with such other types as appeared in F_2.

My experiments, taken together with the cytological observations of Sakamura (21) and Kihara (10), suggested that we have to deal here with a linkage of a higher order due possibly to a definite connection between the chromosomes.

I suggested this idea in my papers of 1925 (14, 15), and recently I have examined closely my data on wheat hybrids which have accumulated for several years past. As a result I have been able to confirm my ideas and can now place them on a larger basis of experimental fact.

I found in the recent paper of Bateson (3) an opinion analogous to my own. For Bateson, examining the results of Engledow's (6) investigations on the cross *polonicum* × *durum*, believes that the "association of characters may be due to an association of particular chromosomes."

Cases of fusions of various kinds between the chromosomes are mentioned several times in the cytological literature. So far as I know, Agar (1) was the first to write on the connection between the chromosomes, these phenomena having been observed by him in the heterotypic metaphase in *Lepidosiren*. He considers the connecting links between the chromosomes as composed of linin, brought into prominence by overstaining, and merely serving to orientate the chromosomes in the heterotype spindle by means of their elasticity.

The connections between chromosomes in root tips of *Galtonia* were

observed by Nawashin (19), who found one pair of small chromosomes constantly attached to the inner end of a certain pair of long chromosomes. Gates (7, 8) has described a case of a temporary fusion of chromosomes in *Lactuca*. In his paper of 1920 he writes that "in the meiotic chromosomes of lettuce is the tendency which appears for certain of the bivalent chromosomes to coalesce more or less completely on the equatorial plate of the heterotypic spindle." "The diminution in number of chromosomes at this time is thus found to be due to the temporary coalescence of two bivalent chromosomes, probably end to end, giving eight bodies, or of two more, diminishing the number to seven bodies." It is suggested by Gates that this coalescence may furnish a basis for the phenomenon of partial coupling or repulsion "apart, altogether, from the crossing-over phenomena, which are based on relations between the two members of a pair of chromosomes in their earlier postsynaptic stages." An analogous case of fusion of two groups of gemini in certain *Pentstemon* species was described by Winge in 1924 (27). The same author (28) found in wheat (a speltoid *Tr. vulgare*) in the heterotypic metaphase "ein grosses, oblong-ringförmiges Chromosom, das, obschon dies nicht unmittelbar einleuchtet, wahrscheinlich aus 3 Chromosomen besteht, die sich in einem Kreise lagern." In another place Winge writes that "in der Metaphase der Reduktionsteilung ab und zu ein Komplex von 3 Chromosomen konjugiert war."

Cases of connection of chromosomes were observed by Woycicki (29) in *Yucca recurva*. In *Yucca* there are chromosomes of different sizes. Strasburger (23) suggested that the small chromosomes are derived from larger ones by fractionation. He said that "die kleinen Chromosomen aus erblich fixirten Querteilungen der grossen abzuleiten, liegt überaus nahe." Woycicki, investigating the equatorial plate in the cells of root tips when photographed with a blue filter, observed that: "la couronne équatoriale n'est pas constituée par les chromosomes libres groupés de la manière, dont l'a dessinée Cl. Müller (18); au contraire, tous les chromosomes sont liés l'un avec l'autre par les trabécules spécifiques, c'est à dire indépendants du fuseau." He also calls attention to the regularity in arrangement of small chromosomes in the equatorial plates of *Yucca*, and to the presence on the figures of Strasburger of fibres uniting the small chromosomes. Further, he suggests that the chromosomes are united in the heterotypic metaphase, and that this connection may play a part in the phenomena of "coupling" and "repulsion."

Miss J. M. Allen (2) has observed the connections between chromosomes in *Matthiola incana*. She writes that "in many cases the bivalent

chromosomes show connecting threads or bands. These connecting links stain deeply with iron-alum-hematoxylin as if composed of chromatin."

It was established by Sakamura that the four species of wheat, namely *dicoccum*, *polonicum*, *durum* and *turgidum*, are tetraploid, each possessing 28 chromosomes, whilst the species *vulgare* and *Spelta* are hexaploid and contain 42 chromosomes. The phenomenon of linkage between factors determining shapes and sizes of glumes obtains so long as we cross species containing equal numbers of chromosomes. But on crossing a tetraploid species with a hexaploid one the linkage ceases to exist. This fact suggests the idea that linkage phenomena are dependent upon intercourse between chromosomes. It was stated by Sax (22) and Kihara (10) that in the crosses *durum* × *vulgare* and *polonicum* × *Spelta* the F_2 plants possessing 28 chromosomes always reproduce the morphological type of the tetraploid parent. The F_2 plants possessing 42 chromosomes, on the contrary, always reproduce the morphological type of the hexaploid parental species. My own observations have shown that the species *Tr. Spelta* obtained in F_2 on crossing *Tr. dicoccum* with *Tr. vulgare* possesses 42 chromosomes. *Tr. Spelta* appearing in F_2 from the cross *Tr. polonicum* × *Tr. vulgare* contains the same number of chromosomes, *i.e.* 42. The species *Tr. dicoccum* appearing in F_2 from the cross *Tr. polonicum* × *Tr. vulgare* possesses 28 chromosomes. All these facts prove that it is the number of the chromosomes that decides the shapes and sizes of glumes and spikelets.

A question arises whether the quality of chromosomes plays a part in the differentiation of species of wheat. Doubtless the constitution of chromosomes of each tetraploid species is of a different quality, and this also holds good for the hexaploid species. Sax (22), dealing with hybrids *Tr. vulgare* × *Tr. durum*, assumes that the 7 additional chromosomes of *Tr. vulgare* determine the distinguishing characters of the common wheats, and that these characters are due either to a reduplication of hereditary factors or to specific factors in these chromosomes. The second of these alternatives seems to me more probable. We know several tetraploid species differing from each other, from the morphological point of view, and it would be impossible to assume that they are all uniform in respect of the genetic constitution of the chromosomes bearing the factors for shapes and sizes of glumes and spikelets.

But the most important conclusion to be drawn from these observations is that the number of the chromosomes, as well as their constitution, plays a significant part in the production of specific differences.

Factors producing specific characters are located in a smaller number

of chromosomes in the tetraploid species than in the hexaploid ones. If we assume that the factors determining shapes and sizes of glumes and spikelets in the tetraploid species are located in a minimum of two non-homologous chromosomes connected one with another we must admit that this minimum is represented by three non-homologous chromosomes in the hexaploid species. These chromosomes are connected, and they pass, therefore, together to the one pole of the dividing cell.

In a pentaploid hybrid the connection between the chromosomes breaks, and for this reason new combinations of chromosomes may originate. We know that in these hybrids 14 gemini and 7 solitary chromosomes may be observed. These solitary chromosomes often remain outside of the new-formed nucleus. The intracellular equilibrium becomes unstable, and the breaking of the hypothetical connections between chromosomes in these circumstances seems to me very probable.

If we admit that the characters of glumes and spikelets are determined by a great number of factors located in several connected chromosomes, the three difficulties I have mentioned above are easy to overcome.

It becomes clear why linkage exists in the cross *vulgare* × *Spelta* and ceases to exist in the crosses *vulgare* × *dicoccum* and *vulgare* × *polonicum*. It is because in both the last-named crosses two sets of chromosomes of different number unite.

It becomes clear why the individuals of the F_2 generation reproducing the morphological type of the tetraploid parent are more numerous than the individuals reproducing the morphological type of the hexaploid parent. It is because the chances of the appearance of a combination of a smaller number of definite chromosomes is greater than the appearance of a combination of a larger number of definite chromosomes[1].

It becomes clear why the F_2 individuals reproducing the parental types are relatively less numerous than the other types appearing in this generation. It is because in the pentaploid hybrids the aggregate of connected chromosomes breaks, and in F_2 the parental combinations of chromosomes, following the laws of chance, must be less numerous than the sum of other combinations.

I shall now examine the results of some crosses between species of wheat in the light of the hypothesis of the connection of the chromosomes outlined above.

[1] Some of the solitary chromosomes of F_1 plants remain outside the newly formed nuclei of the germ cells. This may be one of the causes of the numerical preponderancy of the combinations of two definite chromosomes of one parent as compared with the number of three definite chromosomes of the second parent.

Crosses between Hexaploid Species.

It was stated in my paper of 1914 that *Tr. Spelta* L. crossed with *Tr. vulgare* Host. ("Square head") gives in F_2 generation four types, namely:

(1) *Tr. Spelta*, reproducing the parental type.

(2) Intermediate individuals reproducing the F_1 type.

(3) *Tr. vulgare* with dense ears of the "Square head" type (common "Square head").

(4) *Tr. vulgare* with compact ears (*Tr. compactum* or "club" wheat).

These four types appeared in the ratio 4 : 8 : 3 : 1. The glumes and spikelets of both types, namely "Square head" and "club" wheat are identical. If we consider these two types as constituting one species, namely that of *Tr. vulgare*, we shall obtain the simple Mendelian ratio 1 : 2 : 1 [4 : 8 : (3 + 1) = 1 : 2 : 1]. Hence it follows that the sizes and shapes of glumes and spikelets of each of these two species (*Tr. Spelta* and *Tr. vulgare*) are dependent on one Mendelian factor. Boshnakian (4) also described a simple Mendelian ratio in crosses between *Tr. Spelta* and *Tr. vulgare*. Kajanus (9), too, found a simple ratio 3 : 1 in F_2 from the cross *Tr. vulgare* × *Tr. Spelta*. The plants reproducing *Spelta* type and the heterozygous plants in the F_2 generation were together three times more numerous in the experiments of Kajanus than those reproducing the *vulgare* type. Kajanus supposes that "bei Spelta ein Gen S vorhanden ist das den Spelta-Habitus bewirkt; S ergibt bei den Heterzygoten Dominanz oder Prävalenz gegenüber dem vulgare-Habitus, hat aber bisweilen eine schwächere Wirkung, so dass die Heterozygoten intermediär oder sogar vulgare-ähnlich werden." According to Kajanus the factor S determines the sizes and shapes of glumes of *Tr. Spelta* and also the characteristic long ears of the species. He also states that "die grösseren Aehrchenabstände der Spelta-Formen vom S-Gen direkt hervorgerufen werden, als Folge der spezifischen Wirkung dieses Gens."

According to the theory of chromosomal connection the factors producing the sizes and shapes of glumes of *Tr. Spelta* as well as those of *Tr. vulgare* are located in several connected chromosomes. I do not mean, however, that beyond this complex of connected chromosomes there is not one single factor influencing the sizes and shapes of glumes. I shall call attention later on to cases of the existence of such factors in describing the crosses between tetraploid species.

CROSSES BETWEEN TETRAPLOID SPECIES.

1. *Triticum polonicum* L. × *Tr. dicoccum* Schübl.

This cross gives in F_1 intermediate individuals, and in F_2 a segregation in a simple Mendelian proportion of 1 : 2 : 1. Percival in his Monograph (20) describes the phenomena of segregation in the posterity of such hybrids. He has observed the progeny of a natural hybrid between *Tr. polonicum* and *Tr. dicoccum*. The F_1 ears were intermediate. The F_2 from this gave three clearly differentiated types, viz.:

(1) *Tr. polonicum*, almost typical in form and size of the ear.

(2) A form closely resembling *Tr. dicoccum*.

(3) An intermediate type, nearer in character to the *dicoccum* than to the *polonicum* parent. The types (1) and (2) bred true in the F_3 and F_2 generations; type (3) behaved as the F_1 plant.

In my experiments I have also obtained in F_2 from the cross *polonicum* × *dicoccum* a simple ratio 1 : 2 : 1. I made five crosses of this kind and in F_2 I always obtained three types in the proportion shown in Table I.

TABLE I.

	Number of F_2 individuals		
	Polonicum type	Intermediate type	*Dicoccum* type
Cross No. 1	13	31	13
„ No. 2	14	37	16
„ No. 3	30	62	21
„ No. 4	7	14	7
„ No. 5	7	13	5
Totals	71	157	62
Expectation	72·5	145	72·5
Ratio	1	2	1

In some of these crosses it is, however, easy to distinguish within the limits of each of the three F_2 types two categories of plants, viz. one with long glumes and another with short ones. These two categories of plants appeared in crosses No. 1 and No. 2. Long glumes are dominant to short ones. On Plate XII are shown the ears of *Tr. dicoccum* with long glumes (*a*) and (*b*) and those with short ones (*c*, *d*). On the same Plate are shown two ears of an ordinary *Tr. polonicum* (*e*, *f*) which appeared in the F_2 generation, and two ears of a new type of *Tr. polonicum* with short glumes (*g*, *h*), observed in the same F_2 generation. The F_2 plants with long glumes give in F_3 the same kind of segregation which appeared in F_2, or else they produce individuals with long glumes only. In the crosses No. 1 and No. 2 the individuals of *Tr. dicoccum* with short glumes

(Plate XII, *c*, *d*) were used for crossing as maternal plants. In the F_2 generation, therefore, plants of *Tr. polonicum* type with short glumes occurred. In the other crosses the type of *Tr. dicoccum* with long glumes was employed, and in these crosses *polonicum* with short glumes was not observed.

Fig. 1 represents two families of an F_3 generation from cross No. 1. On the left (Fig. 1, *a*, *b*, *c*) are shown three types of wheat with short

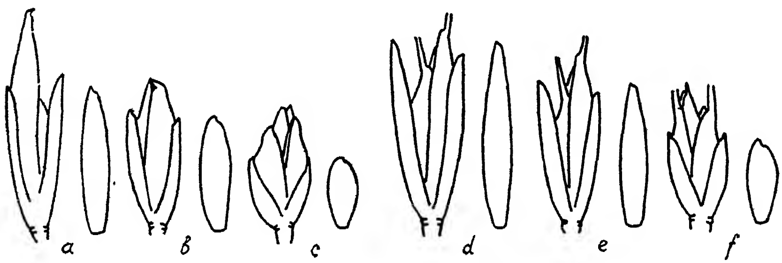


Fig. 1. Spikelets and glumes of F_3 from the cross *polonicum* × *dicoccum*. *a*, *polonicum* with short glumes; *b*, intermediate type with short glumes; *c*, *dicoccum* with short glumes; *d*, *polonicum* with long glumes; *e*, intermediate type with long glumes; *f*, *dicoccum* with long glumes. Magnified 1·6 times.

glumes, namely *polonicum* with short glumes (*a*), intermediate type with short glumes (*b*), and *dicoccum* with short glumes (*c*). On the right of this figure (*d*, *e*, *f*) a family with long glumes is shown. There are represented *polonicum* with long glumes (*d*), intermediate type with long glumes (*e*), and *dicoccum* with long glumes (*f*). The three types represented in Fig. 1, *a*, *b*, *c*, as well as those represented in Fig. 1, *d*, *e*, *f*, occur in the proportion 1 : 2 : 1 (1 *polonicum* : 2 intermediates : 1 *dicoccum*).

Some data concerning the segregation phenomena of the F_3 generation are shown in Table II.

TABLE II.

	Number of individuals of F_3 generation					
	Polonicum with large glumes	*Polonicum* with small glumes	Intermediate with large glumes	Intermediate with small glumes	*Dicoccum* with large glumes	*Dicoccum* with small glumes
91 (1919)	10	—	21	—	8	—
100 (1919)	5	2	12	3	7	1
90 (1919)	—	3	—	7	—	6
98 (1919)	—	5	—	15	—	4
102 (1919)	—	8	—	17	—	10
Totals	33		75		36	
Expectation	36		72		36	
Ratio	1		2		1	

The flowering glumes are of the same length in each of the above-mentioned lines of the F_3 generation, independently of the length of empty glumes.

The segregation phenomena that I have observed in the crosses *polonicum* × *dicoccum* may be explained in the following way.

Let us suppose, that the essential sizes and shapes of empty glumes and spikelets of both *Tr. polonicum* and *Tr. dicoccum* are determined by a complex of linked factors. Beyond this complex and independently of it, there exists one factor that increases the length of the empty glumes. This factor is derived from *Tr. polonicum*, and is inherited independently of the complex of linked factors.

If, on the theory of chromosomal connection, we assume that the linked factors are located in several connected chromosomes, then the factor for increased length will be located in a chromosome unconnected with that group of chromosomes. This factor is therefore inherited independently of those characters, and can be transmitted from the *polonicum* type to the *dicoccum* type, increasing the empty glumes of the latter. Hence in the F_2 generation of hybrids between *polonicum* with long glumes and *dicoccum* with short glumes the new types appear, namely *polonicum* with short glumes and *dicoccum* with long glumes.

It is probable that there exist still other factors influencing in a slight degree the sizes and shapes of glumes. Neither the *polonicum* type nor the *dicoccum* type obtained in F_2 are as uniform as the ordinary species used in crossing. Within the limits of each of these F_2 types one observes individuals with normal glumes as well as plants with narrower glumes. Beyond that there exists a variability concerning the lateral tooth of empty glumes. This variability is greater here than in either of the two parental species. It also is probably caused by distinct factors independent of the hypothetical complex of linked factors. But the differences appearing in F_2 in connection with the width of the empty glumes and the sizes of the lateral tooth are very slight in comparison with the differences found in the length of glumes, determined by the factor mentioned above.

2. *Tr. polonicum* L. × *Tr. durum* Desf.

The crosses between *polonicum* and *durum* were investigated by St Clair Caporn (5) and Engledow (6). Both authors found that the F_1 generation is intermediate in so far as the glume characters are concerned, and that in F_2 a segregation occurs in the proportion of 1 : 2 : 1. The *polonicum* type, however, extracted from the F_2 generation, has shorter glumes, on the average, than the *polonicum* parent. St Clair

Caporn says that "in all probability the extracted pure shorts exhibit much the same sort of alteration in average value of the glume length when compared with the *eloboni* parent (a variety of *Tr. durum*), with the difference that instead of being lowered, the average length is increased."

If we assume that the essential sizes and shapes of glumes of *Tr. polonicum* and *Tr. durum* are determined by factors located in a complex of connected chromosomes, then the factors increasing the length of the glumes would be located in other chromosomes, and they would be inherited independently of that complex. Let us suppose that there exist in the *polonicum* parent two cumulative factors slightly increasing the length of the glumes in relation to their essential length. Without these factors, or with a decreased number of them, the glumes of the *polonicum* type become like those of extracted *polonicum*. The glumes of extracted *durum*, on the contrary, would become slightly longer if the plants of this type possessed the factors for increased length. The increasing action of these factors upon the *durum* glumes is hardly distinguishable.

These phenomena may be, in a certain degree, compared with the inheritance of the factor for increased length found by me in the *dicoccum* × *polonicum* crosses. In my experiments I had to deal with one factor only, whose influence upon the length of glumes was prominently marked. The action of this factor was always greater in the *polonicum* type than in the *dicoccum* type.

Crosses between Tetraploid and Hexaploid Species.

1. *Tr. polonicum* L. × *Tr. vulgare* Host.

The plants of the F_1 generation from this cross are intermediate in respect of the sizes and shapes of glumes and spikelets. In F_2 a segregation occurs; a great number of new types appear, and among them one can distinguish individuals representing the *dicoccum* type, the *durum* type and the *Spelta* type. The parental types appear also in this generation. It is very important to note that in my experiments plants possessing the morphological characters of the tetraploid parent, or of any other tetraploid species, possessed the tetraploid number of chromosomes. The plants reproducing the morphological type of hexaploid parent, or of any other hexaploid species, contained 42 chromosomes.

I counted the number of chromosomes in root tips of four F_3 plants belonging to the following types:

(*a*) *Polonicum*. The ears of this plant are shown on Plate XIV, fig. *e*. The plant belongs to the family No. 11 described below. The number of chromosomes was 28.

(*b*) *Dicoccum*. The ear of this plant is shown on Plate XIV, fig. *a*. This plant belongs to the family No. 11. The number of chromosomes was 28.

(*c*) *Dicoccum*. The ear of this plant is shown on Plate XIII, fig. *f*. The plant belongs to the family No. 4. The number of chromosomes was 28.

(*d*) *Spelta*. The ear of this plant is shown on Plate XV, fig. *c*. The plant belongs to the family No. 13. The number of chromosomes was 42.

Another important fact, observed in the F_2 generation, is that the individuals reproducing the morphological type of the tetraploid parent were always more numerous than those representing the morphological type of the hexaploid parent. Some data concerning the segregation phenomena in an F_2 generation are shown in Table III.

TABLE III.

	Number of individuals in F_2 generation				
Polonicum × *vulgare*	*Polonicum* type	*Dicoccum* type	*Spelta* type	*Vulgare* type	Other types
1 (54, 1922)	9	8	—	3	52
2 (51, 1922)	4	5	—	—	53
3 (50, 1922)	7	5	—	1	79
4 (40, 1919)	4	5	4	1	17
5 (11, 1919)	4	2	1	3	15
6 (12, 1919)	2	2	—	—	9
7 (15, 1919)	1	2	—	—	7
8 (53, 1922)	2	2	—	2	37
9 (52, 1922)	6	4	—	1	69
10 (79, 1922)	2	2	—	—	37
11 (46, 1922)	12	11	2	5	69
12 (47, 1922)	7	5	—	2	43
13 (48, 1922)	4	3	—	2	23
Totals	64	56	7	20	510

In Table III the numbers given concern the frequency of the appearance of individuals of four types, namely *polonicum*, *dicoccum*, *Spelta* and *vulgare*. Besides these the numbers of individuals of other types are included. Among these "other types" plants approaching to the *durum* type may be distinguished. I have not put this type separately in Table III because there are many intermediate forms uniting the *durum* type with the remaining types, and the distinction of it is often very difficult. In the F_2 generation of hybrids ex *polonicum* × *vulgare* semi-sterile plants frequently appear. They are generally of small size. It is a characteristic phenomenon that the plants reproducing the type of known and cultivated species are usually fertile and of normal or nearly normal size, while the other types are semi-sterile or sterile.

It follows from the researches of Kihara (10) that in the progeny of pentaploid hybrids a tendency is observed to maintain the numbers of 28 and 42 chromosomes, and to eliminate other combinations. It was stated by Kihara that "die Chromosomenzahl der Nachkommen der 29–34-chromosomigen Pflanzen sich alljährlich vermindert, bis sie 28 beträgt" and "bei den Nachkommen aus den Vermehrungsgruppen (36–41-chromosomigen) nimmt die Chromosomenzahl früher oder später bis 42 zu."

The plants with 28 and those with 42 chromosomes, or with numbers approximate to these, are commonly fertile, while in the cases of other numbers of chromosomes a total or partial sterility occurs.

I distinguished species of wheat chiefly on the basis of characters concerning glumes and spikelets. In the *Spelta* type, besides these characters, the length of ears is taken into consideration. *Tr. Spelta* possesses characteristic long and loose ears. These long ears always appear in an F_2 generation associated with glumes and spikelets of *Spelta*. The spikelets of *Tr. dicoccum* are more or less closely imbricate on the rachis, a feature peculiar to *Tr. dicoccum*. And this feature was also associated in F_2 with the shapes of glumes and spikelets of *dicoccum* type. With regard to differences in shapes of glumes and spikelets between particular species, I concentrated my attention mainly upon the following characters:

(1) *Tr. dicoccum*. The spikelets are relatively narrow, oval. The empty glumes possess a prominent keel, curved, archlike and running from base to apex. It ends in a curved tooth which varies in length and form in different varieties. The empty glumes are in close touch with the flowering glumes. Their principal tooth is curved towards the middle of the spikelets (Fig. 2, *e*, *f*).

(2) *Tr. durum*. The spikelets of this species are broader than those of *dicoccum*. The empty glumes are narrow. A prominent keel, curved, archlike, runs from the base to the tip. The apical tooth is acute, the lateral secondary tooth in which the strong nerve on the outer face terminates being usually short or missing (Fig. 2 *d*).

(3) *Tr. polonicum*. The spikelets are large, flattened. Empty glumes as long as or longer than the rest of the spikelets, narrow, with two small apical teeth.

(4) *Tr. vulgare*. The spikelets are broad. Empty glumes broad. The keel is prominent only in the upper half of the glumes. Apical tooth in the beardless forms is usually short. The lateral secondary tooth is usually more developed than in *dicoccum* and *durum*. The shapes of spikelets

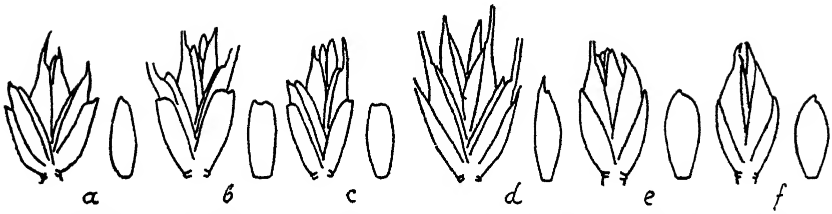


Fig. 2. Spikelets and glumes of four species of wheat. *a, vulgare*; *b, c, Spelta*; *d, durum*; *e, f, dicoccum*. Magnified 1·6 times.

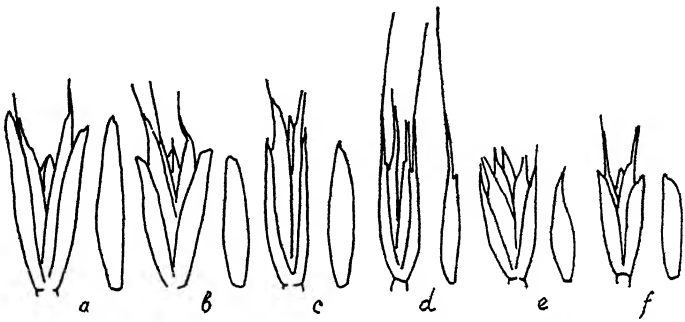


Fig. 3. Spikelets and glumes of the F_2 generation from the cross *polonicum* × *vulgare*. Magnified 1·6 times.

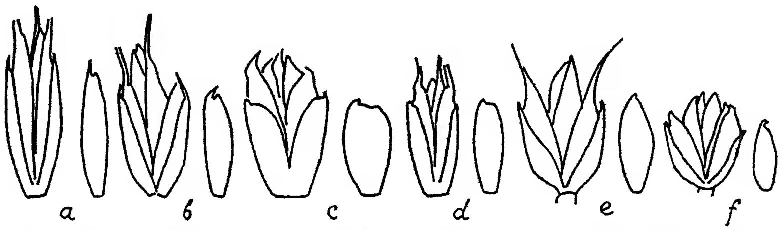


Fig. 4. Spikelets and glumes of the F_2 generation from the cross *polonicum* × *vulgare*. Magnified 1·6 times.

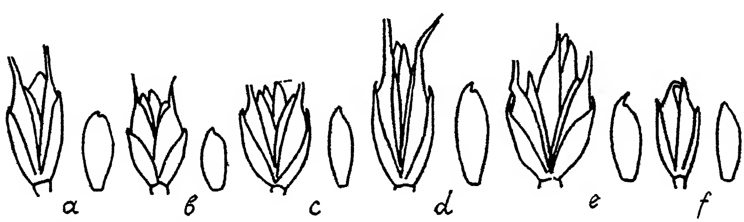


Fig. 5. Spikelets and glumes of the F_2 generation from the cross *polonicum* × *vulgare*. Magnified 1·6 times.

(Fig. 2, *a*) resemble those of *durum*, but they differ distinctly from the shapes of *dicoccum*.

(5) *Tr. Spelta*. The spikelets are convex in section, and in shape resemble a trapezoid, the divergent sides of which are the keels of empty glumes (Fig. 2, *b*, *c*). The shapes of empty glumes resemble a rectangle (Fig. 2, *b*). The keel, which is less prominent than in *dicoccum*, ends in a short blunt tooth. The strong lateral nerve of the glume ends in a blunt projection, which is always much farther away from the base of the apical tooth than is the corresponding secondary tooth in *dicoccum*, *durum* or *vulgare*.

I have already dealt with the fact that in the F_2 generation from *polonicum* × *vulgare* a great diversity of forms appears. Figs. 3, 4, 5 give some idea of the variability of the F_2 generation from this cross. We can recognise the shapes of glumes and spikelets of *polonicum* (Fig. 3, *a*, *b*), *dicoccum* (Fig. 5, *a*, *b*, *f*), *durum* (Fig. 5, *e*), *Spelta* (Fig. 4, *c*, *d*), *vulgare* (Fig. 4, *e*), and also shapes differing more or less from those species. Fig. 3, *c*, *d* and Fig. 4, *a*, represent glumes approaching the *polonicum* type. The glumes represented on Fig. 3, *f*, approach to *dicoccoides*, to *dicoccum* (Fig. 5, *c*, *d*), to *vulgare* (Fig. 4, *f*). Some plants possess glumes with short teeth (Fig. 3, *b*; Fig. 4, *d*), others with long ones (Fig. 3, *d*; Fig. 4, *a*), etc.

It must be emphasised that F_2 plants considered as belonging to *polonicum* type, *dicoccum* type, etc., differ more or less from the typical *polonicum*, typical *dicoccum*, etc. These differences, however, concern secondary characters of the glumes and spikelets. Notwitshtanding these differences the essential sizes and shapes, distinguishing the species of wheat, are easy to recognise, especially in *polonicum*-, *dicoccum*- and *Spelta*-types. Plants reproducing typically parental species are relatively rare. I have shown on the drawings of Figs. 3–5 the variability of the F_2 generation from one cross. There exist, however, some differences between particular crosses concerning this variability. In certain crosses one observes typical *Spelta* individuals, in others "Spelta" plants approach only more or less to the *Spelta* type. The same may be observed with regard to other types. In the F_3 generation the types in question always emerged in their typical form in my experiments.

The facts above described might be explained by means of the theory of chromosomal connection in the following way.

It was already mentioned that in the tetraploid species a minimum of 2 non-homologous chromosomes are connected, and that in the hexaploid species this minimum consists of 3 connected chromosomes. It is

obvious that the question concerns the gametophyte number of chromosomes. It means that every germ cell of tetraploid species possesses 2 connected chromosomes and every germ cell of hexaploid species contains 3 such chromosomes. These chromosomes are of different genetic constitution. Taking into consideration the facts of the appearance of the species *dicoccum*, *durum* and *Spelta* among the progeny of the hybrids from *polonicum* × *vulgare* we may assume that the chromosomes determining the glumes and spikelets of the three first-mentioned species are present in the parental species, but in other combinations.

If, for instance, the germ cells of *polonicum* possessed the chromosomes **a** and **b**, connected with one another, and the germ cells of *vulgare* contained the chromosomes **c**, **d** and **e**, then the combination **acac** might produce the species *dicoccum*, the combination **cdcd** the species *durum*, and the combination **aceace** the species *Spelta*.

The question arises, why the two chromosomes (sporophyte number = 4 chromosomes) producing the glumes and spikelets of any tetraploid species are always accompanied by other chromosomes in a number complementary to 14 (sporophyte number 28), and why the three chromosomes (sporophyte number = 6) determining the glumes and spikelets of hexaploid species are associated with a number of other chromosomes complementary to 21 (or sporophyte number 42). It might be possible to explain this phenomenon by supposing that the germ cells containing other combinations of chromosomes are unable to perform fertilisation; or, perhaps, by supposing that there exists an unknown affinity between certain chromosomes.

Notwithstanding the great heterogeneity of forms in the F_2 generation there are several regularities in the segregation phenomena in both F_2 and F_3 generations. These regularities are:

(1) The plants reproducing the tetraploid parental type are always more numerous in F_2 than the individuals representing the hexaploid parental type. It follows from the data shown in Table III that in F_2 of 13 crosses between *polonicum* and *vulgare* the plants of *polonicum* type appeared to the number of 64, and those of *vulgare* type to the number of 20. In the Introduction I tried to explain this numerical preponderancy of tetraploid parental types.

(2) In the self-fertilised strains of the F_3 generation showing the segregation into two species, I always found either two tetraploid or two hexaploid species. Besides, these species usually appeared in a simple Mendelian ratio. In the crosses in question, I observed segregations between the species *durum* and *polonicum*, or between *dicoccum* and

polonicum, or between *vulgare* and *Spelta*, but I never saw a strain containing, for instance, both *dicoccum* and *vulgare*, or both *polonicum* and *Spelta*. The segregating pairs of species usually appeared in particular strains of the F_3 generation in the proportion of 1 : 2 : 1. These phenomena seem to indicate that the connections between the chromosomes get restored, and that these connections occur in F_2 and F_3 generations in a greater number of chromosome combinations than were the number of combinations of the two parental species.

(3) In F_3 strains composed of individuals belonging to one species only, the phenomena of continuous variation occur, and may be explained by the action of cumulative factors.

I may now examine more closely the segregation phenomena in certain F_3 families.

Family No. 1 (96, 1923). All the 25 plants of this family belong to the *polonicum* type. Empty glumes are relatively narrow. The principal

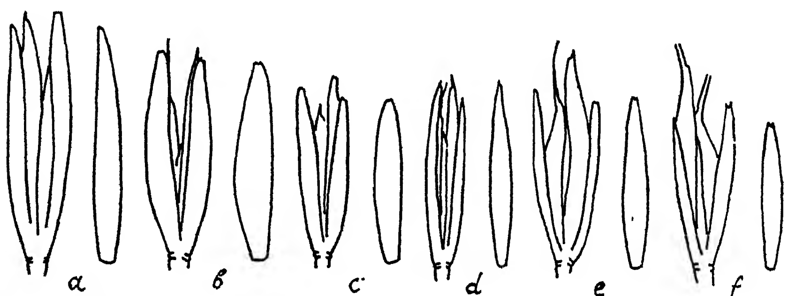


Fig. 6. Spikelets and glumes of a family of the F_3 generation from the cross *polonicum* × *vulgare*. All the plants represent the *polonicum* type. Magnified 1·6 times.

tooth is short (Fig. 6, *a*, *b*). Several individuals possess empty glumes remarkably shorter than the flowering glumes (Fig. 6, *e*, *f*). Empty glumes of other plants are as long as the flowering glumes or longer (Fig. 6, *a*, *b*). Plants in this family are with a long and a short straw. Some differences arise also in the sizes of spikelets. There are plants with large spikelets (Fig. 6, *a*) and others with small ones (Fig. 6, *c*, *d*). There are also plants with wide spikelets (Fig. 6, *b*, *c*) and others with narrow ones (Fig. 6, *d*).

Family No. 2 (94, 1923). All the 23 plants belong to the *polonicum* type. Empty glumes are narrow here. The principal tooth is longer than in the preceding family and usually crooked (Fig. 7, *a*, *b*, *c*, *d*, *e*). The length of the empty glumes is relatively smaller here than in the pre-

ceding family. Plants with empty glumes considerably shorter than the flowering glumes are numerous (Fig. 7, *d*). Differences in sizes of spikelets occur also in this family.

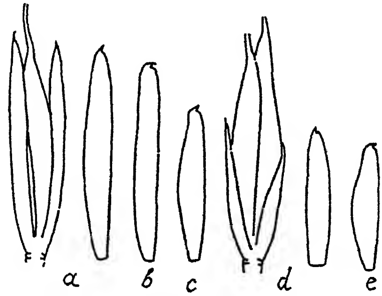


Fig. 7. Spikelets and glumes of an F_3 family from the cross *polonicum* × *vulgare*. *a*, *b*, spikelet and glumes of *polonicum* with long glumes; *c*, *d*, *e*, spikelets and glumes of *polonicum* with short glumes. Magnified 1·6 times.

Family No. 3 (15, 1922). All the 15 plants belong to the *dicoccum* type. It is a *dicoccum* with short glumes, near to that represented on Plate XII, *c*, *d*. The tooth is large, the glumes hard. There are plants with large spikelets and glumes, and others with small ones. Also there are some differences in the width of the spikelets and in their sizes.

Family No. 4 (7, 1922). All the 22 plants of this family belong to the *dicoccum* type with long glumes. Four ears of this family belonging to four different plants are shown on Plate XIII, *d*, *e*, *f* and *g*. The tooth is long and generally obtuse. Sometimes, however, it is sharp like that of the *dicoccum* type. There are also some differences concerning the shapes of the glumes. Some individuals possess narrow glumes, others have the glumes widened in the middle part. Some types of glumes and spikelets of this family are shown in Fig. 8, *a*, *b*, *c*, *d*, *e*, *f*.

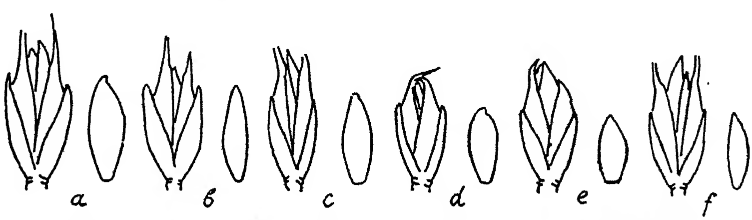


Fig. 8. Spikelets and glumes of an F_3 family from the cross *polonicum* × *vulgare*. All the plants belong to the *dicoccum* type. Magnified 1·6 times.

Family No. 5 (14, 1922). All the 15 plants of this family approach the *dicoccum* type. But some characters of the *polonicum* type are often to be recognised here. Some plants possess glumes and spikelets longer

than in ordinary *dicoccum*. These deviations towards the *polonicum* type are slight and the plants do not pass beyond the limits of the *dicoccum* type. The glumes are always hard.

Family No. 6 (98, 1923). The whole family possesses the ears of the *dicoccum* type. The glumes, however, are relatively narrow and straight here. The shapes of spikelets deviate slightly in the direction of *vulgare*. The glumes are hard.

Family No. 7 (95, 1923). This family embraces the species *dicoccum* and *polonicum*, together, of course, with intermediate types. Within the limits of each of the two species considerable variability is to be observed, and analogous variation is also characteristic of the intermediate class of plants. A peculiar feature of this family was the hardness of all individuals. Even the glumes of *polonicum* type were relatively hard.

Family No. 8 (100, 1923). This family embraces plants of both *dicoccum* and *polonicum* types, and also individuals of intermediate shapes. In all there were 16 plants. The scale of variation of this family is greater than in the preceding family. All the plants possess glumes relatively soft, even the plants of the *dicoccum* type.

Family No. 9 (17, 1922). This family is composed of plants of two types—*polonicum* and *dicoccum*. There are, of course, intermediate individuals. The individuals of the *dicoccum* type here possess wide spikelets and deviate in the direction of the *durum* type. All the plants (including those of the *polonicum* type) possess hard glumes.

Family No. 10 (6, 1922). The family contained 36 plants belonging to both *polonicum* and *dicoccum* types, and was relatively uniform. For that reason the segregation into *polonicum*, intermediates and *dicoccum* in the ratio of 1 : 2 : 1 is here very clear and indisputable.

Family No. 11 (4, 1922). Some ears of this family are shown on Plate XIV. There are ears of the *dicoccum* type, of the *polonicum* type and of other types approaching more or less either to *dicoccum* or to *polonicum*. The ears *a* and *b* may be considered as belonging to the *dicoccum* type. The ear *c* is intermediate. The ears *d*, *e*, *f* and *g* represent the *polonicum* type either with long glumes (*d*) or with short ones (*g*). The ear *h* on this plate represents a peculiar type with glumes and spikelets of a magnified *dicoccum* type. The shapes of glumes and spikelets are really those of *dicoccum*. With regard to their shapes they are very much like those of the ear *a*. But their sizes are larger. This family contained 40 plants which may be classified in three groups, namely, *dicoccum*, intermediates and *polonicum*. The *polonicum* individuals formed one-fourth, on the average, of the total number of plants of this family.

Family No. 12 (102, 1923). This family comprised two types appearing in the 1 : 2 : 1 proportion, namely, 6 plants of *polonicum* type, 17 intermediate plants and 9 individuals of *durum* type. Both types, *polonicum* and *durum*, are relatively uniform here. Three ears of the *durum* type belonging to three different plants are shown on Plate XIII, *a*, *b*, *c*. One spikelet and one glume of ear *b* are represented in Fig. 9, *a*.

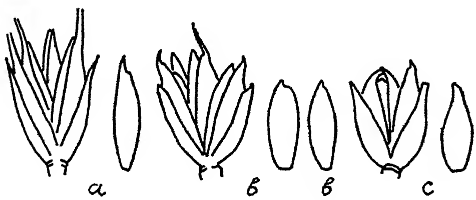


Fig. 9. Spikelets and glumes of three F_3 families from the cross *polonicum* × *vulgare*. *a*, *durum* type; *b*, *vulgare* type; *c*, *vulgare* type with the glumes resembling a bottle. Magnified 1·6 times.

Family No. 13 (12, 1922). This family contained only *Spelta* individuals. The glumes here were always hard, and the ears long and lax. Two ears of this family, belonging to two different plants, are represented on Plate XV, *b*, *c*. One spikelet and one glume of the ear *c* is shown in Fig. 10, *a*. The spikelets and glumes of other plants of this family are shown in Fig. 10, *b*, *c*, *d*, *e*.

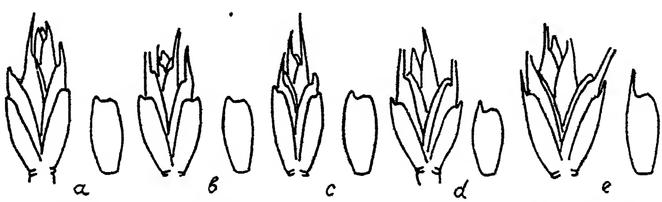


Fig. 10. Spikelets and glumes of an F_3 family from the cross *polonicum* × *vulgare*. All the plants belong to the *Spelta* type. Magnified 1·6 times.

Family No. 14 (5, 1922). This family contained *Spelta* individuals. The *Spelta* type is here somewhat impure. There were in almost every individual some elements of the *polonicum* type. This is shown on Plate XV, *a*, *d*, *e*, *f*. The ears are here long and lax, the spikelets hard, but the glumes usually longer than in the pure *Spelta* type. They conserve, however, the lateral tooth prominently marked and the shapes of them usually approach a rectangle (*d*, *e*).

Family No. 15 (160, 1923). This family contained only *vulgare* individuals. The glumes here were soft. The shapes of the glumes are

usually typical. One spikelet and two glumes of one *vulgare* individual of this family are shown in Fig. 9, *b*.

Family No. 16 (97, 1923). The plants of this family resemble those of *vulgare* type. The ears are soft, and the glumes are bottle-shaped (Fig. 9, *c*). This family is rather uniform so far as the shapes of the glumes are concerned.

The data recorded above prove that the segregation phenomena in the crosses *polonicum* × *vulgare* cannot be altogether explained on the assumption of spontaneous combinations of chromosomes, which were connected in the parental species. On this assumption we may explain the apparition of the new species in the F_2 generation—we may explain the numerical preponderancy in the F_2 generation of the morphological type of the tetraploid parental species, and finally the segregation into two tetraploid species or into two hexaploid ones, in the particular families of the F_3 generation. But the scale of variation is larger in reality than it would be if *all* the factors determining the shapes of glumes and spikelets had been located in the connected chromosomes. It is obvious that the semi-sterile chromosomal combinations do not remain without influence on the variation. Nor is the possibility excluded that in wheat also "crossing-over" phenomena in Morgan's sense exist, and that in a certain degree they increase the scale of variation.

2. *Tr. dicoccum* Schübl. × *Tr. vulgare* Host.

The F_1 plants were intermediate in respect of the sizes and shapes of the glumes and spikelets. In F_2, in addition to the parental types and many intermediate forms, there appeared also plants resembling the *Spelta* type, and other plants resembling the *durum* type. The most numerous were the individuals of the *dicoccum* type, or those nearly approaching to it. The plants reproducing closely the parental species were very rare. In Table IV are shown the numbers concerning the frequency of occurrence of plants belonging to different types.

TABLE IV.

Dicoccum × *vulgare*	Number of individuals in F_2 generation				
	Dicoccum type	*Durum* type	*Spelta* type	*Vulgare* type	Other types
1 (67, 1922)	7	—	—	2	55
2 (64, 1922)	11	4	2	—	14
3 (70, 1922)	4	3	1	—	19
4 (69, 1922)	12	5	2	3	50
5 (66, 1922)	7	3	4	3	40
6 (71, 1922)	15	8	4	2	58
Totals	56	23	13	10	236

I have taken into consideration only the crosses in which the species *dicoccum* with short glumes (Plate XII, *c*, *d*) was employed. Other crosses made with *dicoccum* with long glumes gave the segregations resembling those observed in the crosses *durum* × *vulgare*.

The F_2 plants of the *dicoccum* type have 28 chromosomes and those of *vulgare* type 42 chromosomes. The same number of chromosomes (viz. 42) also characterises the individuals of the *Spelta* type which appeared in this generation. This is an important fact, for it proves that *Spelta* represents a compound type dependent on the presence of a definite number of chromosomes. The F_2 plants belonging to the *Spelta* type possess characteristic lax ears and broad truncate empty glumes of which the lateral nerve ends in a blunt secondary tooth some distance away from the keel tooth. All these characters appear together on the individual plants of the F_2 generation, and on examining such plants I found 42 chromosomes in their root cells. I took for cytological investigation only quite typical *Spelta* forms, and counted the number of chromosomes in two such F_2 plants.

The synthetic *Tr. Spelta* crossed with *Tr. vulgare* gives in F_2 a segregation in the proportion of 1 *Spelta* : 2 intermediates : 1 *vulgare*. It behaved therefore in this respect like the cultivated varieties of this species.

The segregation phenomena in the F_3 generation have shown the same regularities which were observed in the cross *polonicum* × *vulgare*. With regard to the segregation into particular species I have observed only the segregations either into *Spelta* and *vulgare* or into *dicoccum* and *durum*. I have investigated 52 F_3 families, but I never noticed a segregation between *Spelta* and *dicoccum*, or between *vulgare* and *dicoccum*. F_3 families representing the parental types were not uniform. Little differences in sizes and shapes of glumes and spikelets appear between particular plants of each family like those observed in the corresponding families of the cross *polonicum* × *vulgare*. These differences are hereditary, and it is possible that we have to deal here with the action of cumulative factors. However, I shall not enter into details, leaving the examination of these phenomena for a later paper.

3. *Tr. polonicum* L. × *Tr. Spelta* L.

The degree of sterility of these hybrids is relatively high, and therefore one obtains but a small number of F_2 plants. I secured only 48 F_2 plants as the progeny of 3 F_1 hybrids. Among these were 6 plants representing the *polonicum* type and 1 individual only that I could consider

as belonging to the *Spelta* type. In addition I found 5 individuals of the *dicoccum* type. Other plants of this progeny represented diverse types which I was unable to identify with the known species of wheat. In Table V the numbers concerning this segregation are shown.

TABLE V.

Polonicum × *Spelta*	Number of indidividuals of F_2 generation			
	Polonicum type	*Dicoccum* type	*Spelta* type	Other types
1 (118, 1925)	3	2	—	12
2 (119, 1925)	2	2	—	10
3 (120, 1925)	1	1	1	14
Totals	6	5	1	36

In Fig. 11 the shapes of spikelets and glumes are shown belonging to *polonicum* type (a, b), *dicoccum* type (c, e) and *Spelta* type (d). This last drawing concerns a plant which is not quite typical *Spelta*. The spikelets are here too narrow, and the glumes too long, when compared with the normal *Spelta*. But in the shapes of glumes and the firm and

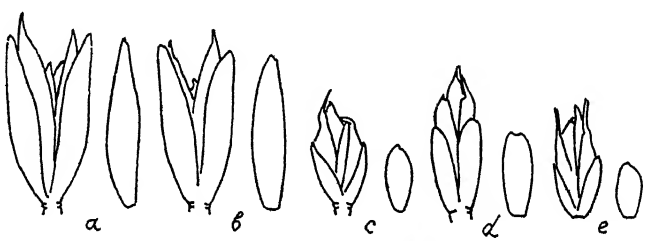


Fig. 11. Spikelets and glumes of the F_2 generation from the cross *polonicum* × *Spelta*. *a, b, polonicum* type; *c, e, dicoccum* type; *d*, spikelet and glume approaching to *Spelta* type. Magnified 1·6 times.

lax ears this individual approaches the *Spelta* type. The plant, whose spikelet is shown in Fig. 11, *c*, may be regarded as typical *dicoccum*. The *polonicum* individuals are here very near to the typical *polonicum*. As in the previous crosses the F_2 plants representing the tetraploid parental type are here also more numerous than those representing the hexaploid parental type.

4. *Tr. dicoccum* Schübl. × *Tr. Spelta* L.

I could distinguish in the F_2 generation two species: *dicoccum* and *Spelta*. There were also other F_2 plants, usually sterile or semi-sterile, whose morphological characters were, however, not so prominent as those separating the species of wheat. Some of these "other plants" had

narrower glumes or smaller ears than *dicoccum* or *Spelta*, or they had the shapes of glumes and spikelets slightly modified. They generally approached one or other parental species, but there was among them no plant which could be identified with any other species of wheat. The

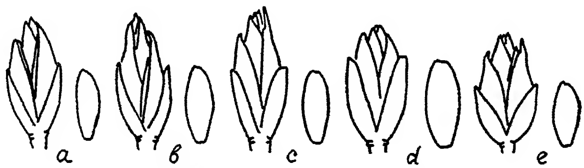


Fig. 12. Spikelets and glumes of the F_2 generation from the cross *dicoccum* × *Spelta*. Plants of *dicoccum* type or approaching more or less to that type. Magnified 1·6 times.

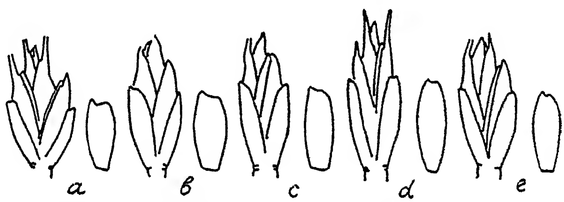


Fig. 13. Spikelets and glumes of F_2 from the cross *dicoccum* × *Spelta*. Plants of *Spelta* type or approaching to that type. Magnified 1·6 times.

F_2 plants classed as *dicoccum* or *Spelta* were not so uniform as the parental species. Figs. 12 and 13 give some idea of the variability of these two types in the F_2 generation. The numbers concerning the frequency of occurrence of the two types are shown in Table VI.

TABLE VI.

	Number of individuals of F_2 generation		
Dicoccum × *Spelta*	*Dicoccum* type	*Spelta* type	Other plants
1 (141, 1925)	12	5	19
2 (140, 1925)	6	2	16
3 (139, 1925)	5	1	14
4 (138, 1925)	7	2	9
5 (136, 1925)	7	—	16
6 (137, 1925)	8	—	7
Totals	45	10	81

As in other crosses between tetraploid and hexaploid species, the individuals reproducing the morphological type of the tetraploid parental species are also more numerous in the present cross than the plants reproducing the morphological type of the hexaploid parent.

If the plants designated "other plants" were classified into categories

according to their resemblance to one or to another of the parental species, we should obtain only two groups of plants, namely:

(1) Plants of *dicoccum* type or approaching more or less to that type.

(2) Plants of *Spelta* type or approaching to that type.

Spikelets and glumes of some plants of the first category are shown in Fig. 12 and those of the second in Fig. 13.

The results are analogous here to those observed in the crosses *durum* × *vulgare*. Kihara (10) writes that the progeny of F_1 hybrids of such crosses segregate "in zwei Gruppen, erstens in die vulgare-Form (eingeschlossen die annähernd vulgare-Form aufweisenden Pflanzen) und zweitens in die durum-Form (inkl. die angenäherten durum-Formen)." From the numbers given by Sax (22) for the segregation phenomena in the crosses *durum* × *vulgare* one can deduce that plants possessing the shape of spikelets of *durum* were in the experiments of this author more numerous than the individuals with the shape of spikelets of *vulgare*. It follows also from the data given by Thompson (24) that the F_2 plants of *durum* type were more numerous in his cross *durum* × *vulgare* than the individuals of the *vulgare* type. Among the 57 F_2 plants Thompson found 28 individuals with the glume shape of *durum*, 10 individuals with the glume shape of *vulgare*, and 19 intermediate plants.

Conclusions Concerning the Relationship between Species of Wheat.

The phenomenon of the occurrence in an F_2 generation of various species beside the parental types proves that the parental types contain the elements determining those species. If we assume that these elements are chromosomes, then the various combinations of them could produce all the species in question. We have admitted that in the tetraploid species 2 chromosomes, and in the hexaploid 3 chromosomes are connected. Since in these connected chromosomes are located factors for specific characters, it is possible that a hexaploid species might possess 2 chromosomes in common with a tetraploid one. Consequently, in certain crosses we should obtain less complicated segregations than in others.

In my experiments the most complicated segregations have appeared in the crosses *polonicum* × *vulgare* and the least complicated in the crosses *dicoccum* × *Spelta*. From the results of my experiments and of those of other authors I shall try to find the degrees of relationship between particular species of wheat.

Tschermak (25) has classified the species of wheat into three groups

according to the degree of fertility observed after crossing. These groups are as follows: I. *Tr. monococcum*; II. *Tr. durum*, *Tr. turgidum*, *Tr. diccocum*, *Tr. polonicum*; III. *Tr. vulgare*, *Tr. Spelta*.

Vavilov (26) found that the immunity to rust is different in those three groups. This author classes *Tr. monococcum* as immune to rust, and *Tr. durum*, *turgidum* and *polonicum* as resistant, although *dicoccum* has both resistant and susceptible forms. The species *vulgare* and *Spelta* are classed as susceptible.

Sakamura (21) stated that these groups differ from one another in the number of chromosomes.

The three groups are most distinctly separated by the number of chromosomes. But the number of chromosomes cannot prejudice their genetic constitution, which may be different in every species. It is probably for that reason that within the limits of each group the relationships of sterility and immunity will show lesser or greater differences. The fact of the existence of *Tr. dicoccum* races both susceptible and immune to rust indicates that the causes of immunity do not depend upon the number of chromosomes but on the genetic constitution of particular races. In any case the number of chromosomes cannot be the only source of differences in the degree of immunity. Then in the survey of the degree of fertility given by Tschermak we find that the different species belonging to one of two definite groups may show certain differences after crossing. Thus the hybrids between "Emmer-Nackttypen" and "Dinkel-Spelztypen" according to Tschermak's experiments are "abgeschwächt oder völlig fertil," the hybrids between "Emmer-Spelztypen" and "Dinkel-Spelztypen" are "abgeschwächt fertil," whilst the hybrids between "Emmer, normale Nackttypen" and "Dinkel, normale Nackttypen" are "völlig fertil." Under the name of "Emmer" Tschermak groups all the tetraploid species of wheat, and under the name of "Dinkel" the hexaploid ones.

The degree of sterility of pentaploid hybrids is different in different crosses. It depends, therefore, not only upon the meeting in one individual of two unequal sets of chromosomes, but also upon the genetic constitution of these chromosomes. Thompson (24) came to a similar conclusion, namely, that in the F_1 hybrids "the 14 *durum* chromosomes or 21 *vulgare* chromosomes work together properly, but the differences between them are so great that combinations of the two sorts may be incompatible."

The calculation of the degree of sterility is based on the number of grains found in the ears of hybrids. But the number of grains in individual spikelets is greater in *vulgare* than in *dicoccum* or *Spelta*. These differences

exert an influence upon the F_1 generation. One cannot, therefore, compare directly the degree of sterility of two F_1 hybrids obtained from different crosses. In my experiments, for instance, the degree of sterility of F_1 plants from the cross *durum* × *Spelta* was approximately the same as in the hybrids of *polonicum* and *dicoccum*. But the sterility of the last-named hybrids must be considered as relatively greater because the grains in both *polonicum* and *vulgare* are more numerous than in *dicoccum* or *Spelta*. And it is just in the crosses *polonicum* × *vulgare* that the F_2 generation showed a greater diversity of forms than in the crosses *dicoccum* × *Spelta*.

It is probable that the higher degree of fertility in the latter cross (in comparison with that in the former) is due to the meeting of a certain number of similar or identical chromosomes. And it is probable also that the fact of the existence of such chromosomes in a given pair of crossed species is the principal cause of a relatively small heterogeneity in the F_2 generation of some pentaploid hybrids.

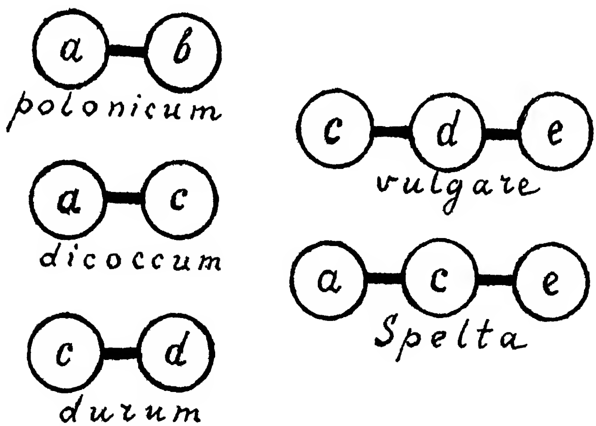
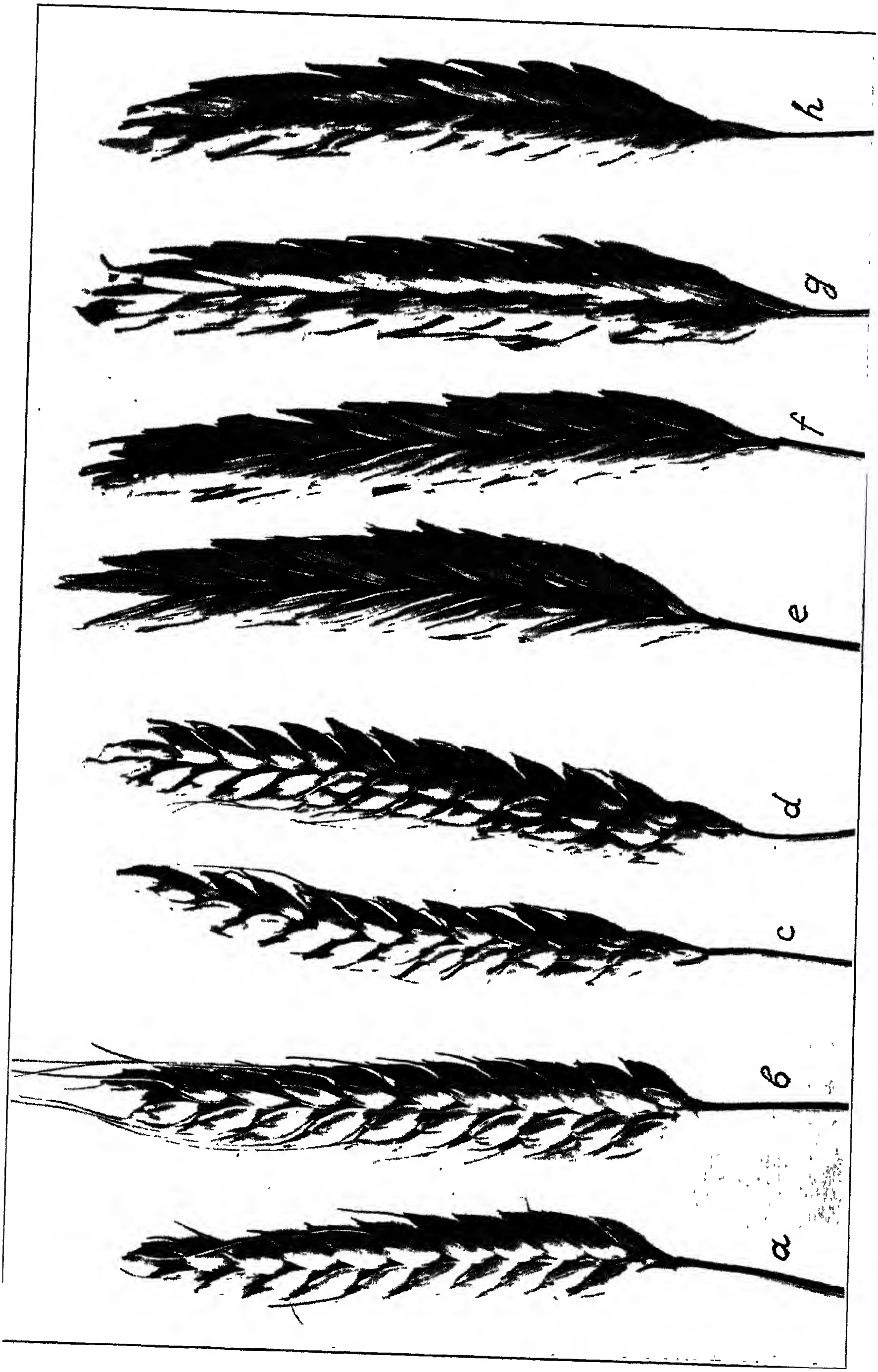


Fig. 14. Scheme representing the supposed relationships between five species of wheat.

The cross *polonicum* × *vulgare* has given in my experiments the greatest heterogeneity as regards the F_2 generation, and I have observed the smallest in the cross *dicoccum* × *Spelta*. This difference in the degree of heterogeneity may indicate that the species *dicoccum* and *Spelta* have certain chromosomes in common.

Let us suppose that *polonicum* contains two connected chromosomes **a** and **b**, *dicoccum* two connected chromosomes **a** and **c**, and *durum* **c** and **d**. Since *vulgare* crossed with *durum* gives a relatively uniform F_2 generation, we may assume that these two species have the chromosomes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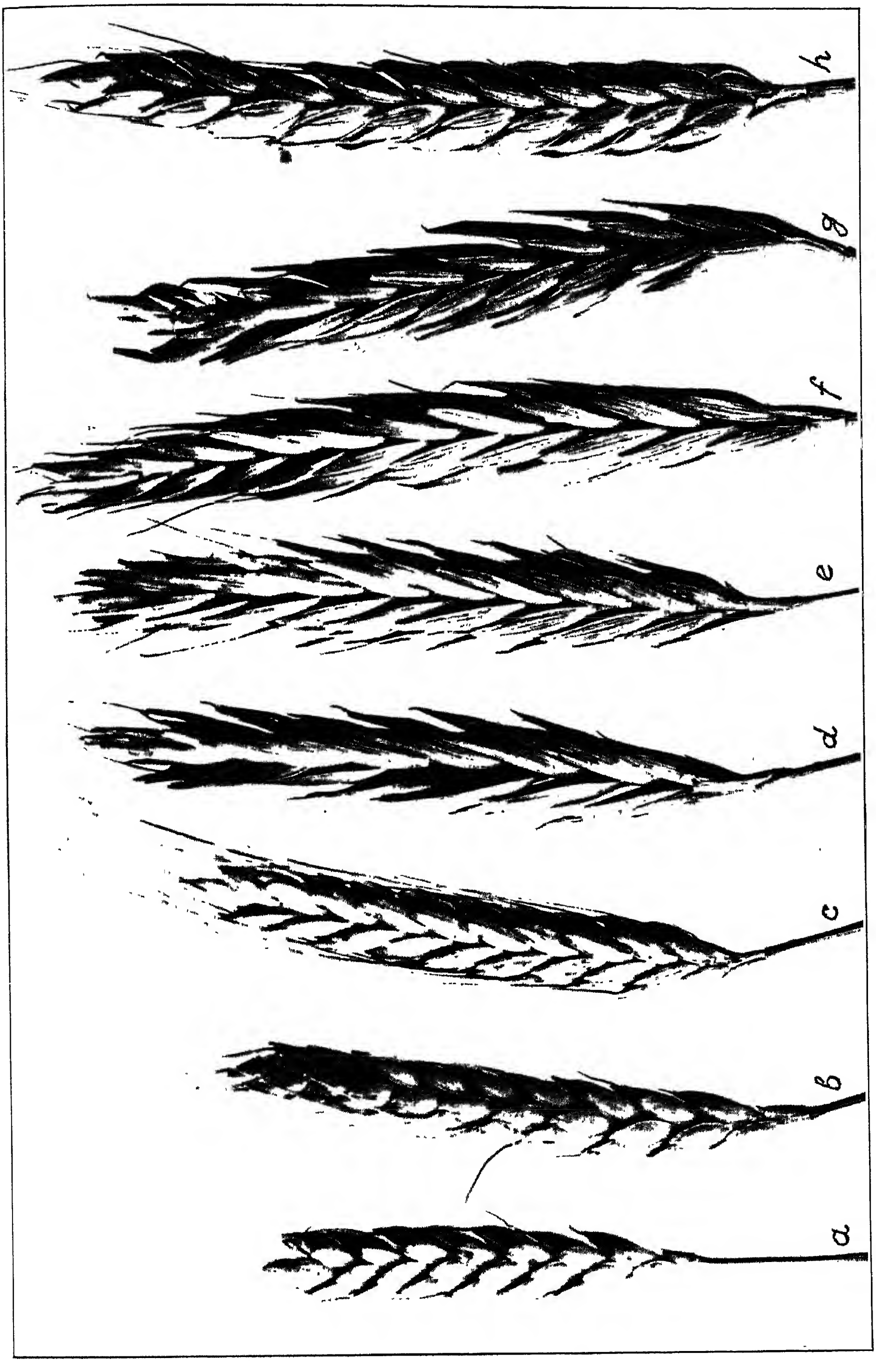
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c and **d** in common and that *vulgare* contains in addition the **e** chromosome. *Spelta* crossed with *dicoccum* also gives a small heterogeneity in F_2. We may assume, therefore, that *Spelta*, in common with *dicoccum*, possesses two chromosomes **a** and **c**. The variation of the F_2 generation from the cross *polonicum* × *vulgare* is greater than in the cross *dicoccum* × *vulgare*. For that reason we may assume that if *polonicum* has not one single chromosome common with *vulgare*, there must exist at least one common chromosome (for instance, **c**) in *dicoccum* and *vulgare*. Fig. 14 shows the supposed relationships between five species of wheat, namely *polonicum*, *dicoccum*, *durum*, *vulgare* and *Spelta*.

In considering the relationship of wheats I have taken into consideration chiefly the sizes and shapes of glumes and spikelets.

It is obvious that beyond the complexes of connected chromosomes in each species, factors influencing shapes of glumes may exist and a complete reconstruction of parental species in the posterity of pentaploid hybrids may therefore in such circumstances be difficult to obtain. If the factors in question really exist they are probably more numerous in hexaploid species because these species contain a greater number of chromosomes. The existence of these factors still further diminishes the chances of appearance of the hexaploid parental types as compared with those of the tetraploid ones. The segregation phenomena are in reality more complicated than they would be if all the factors determining the specific differences were located only in two or three connected chromosomes.

EXPLANATION OF PLATES XII—XV.

The ears of wheat shown on these Plates are all of the natural size.

PLATE XII. *a, b*—*Triticum dicoccum* with long glumes. *c, d*—*Tr. dicoccum* with short glumes. *e, f*—*Tr. polonicum* with long glumes. *g, h*—*Tr. polonicum* with short glumes.

PLATE XIII. *a, b, c*—ears of *durum* type belonging to a family of F_3 generation of the cross *Tr. polonicum* × *vulgare*. *d, e, f, g*—ears of *dicoccum* type belonging to a family of F_3 generation of the cross *Tr. polonicum* × *Tr. vulgare*.

PLATE XIV. Ears belonging to a family of F_3 generation of the cross *Tr. polonicum* × *Tr. vulgare*.

PLATE XV. Ears of *Spelta* type belonging to F_3 generation of the cross *Tr. polonicum* × *Tr. vulgare*.

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THE MORPHOGENETICAL VALUE OF THE WEIGHT OF RABBITS AT BIRTH.

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(With Four Text-figures.)

CONTENTS.

Introduction.

As stated before, the weight of rabbits at birth is governed by two different sets of factors. Firstly, by "external" conditions of the growing foetus, such as the age and the nourishment of pregnant females, the duration of the gestation period (Kopeć (12)) and the size of the litter (Kopeć (12), Hammond (7)), and secondly by internal genetic agencies, the action of which was demonstrated by methodical crosses between breeds differing in size (Kopeć (11)). The simultaneous action of both these kinds of factors was most clearly demonstrated in my former experiments on the offspring of Himalayan does mated to a Himalayan and a Silver buck during one and the same rutting time, the latter belonging to a heavier breed (Kopeć (10)). According to genetical differences, the weight of new-born hybrids in these cases was usually greater than that of Himalayan youngsters. But, at the same time, probably by an introduction of specific substances through the body of the doubly mated female from foetuses of one physiological type to foetuses of the other type, the Himalayan born from these matings were as a rule heavier than the normal young of the breed. The hybrids from heterogeneous gestations weighed also more than the F_1 new-born from normal crosses.

The problem now arises, whether and to what extent the influence of both kinds of factors specified above, determining the weight of the new-born rabbits, can be detected during growth and in the adult animals. To this end, the morphogenetical value of the weight of new-born mam-

mals should be taken into consideration. The genetic aspects of the above question have not been, as far as I know, worked out till now. The opinions of breeders concerning the significance of the weight of different domestic animals at birth are still very contradictory. The ultimate solution of this question has also considerable theoretical interest. For if it could be made evident that the weight of the newly born is correlated with the weight of the adult, then my method of studying the inheritance of birth-weight could successfully replace the method hitherto employed of working with full-grown mammals, a considerably more expensive and in some respects less exact method (cf. Kopeć (11), pp. 243–244).

According to MacDowell (14) and also to Punnett and Bailey (15) there is no significant connection between the size of the litter, the age of the doe, the season of birth and the weight of the full-grown rabbits. Castle (2) emphasises that rabbits weighing more on the 29th day of life than others can in the course of time become lighter than others and *vice versa*. But such a possibility, according to my opinion, excludes in no way the existence of an essential positive correlation between the weight of the new-born rabbit and that of the fully developed adult. On the contrary, a distinct positive connection between the weight of growing animals and the weight of young ones may be inferred from other observations. Dunn (3), in her investigations on 7 albino rats, stated that individuals weighing the most on the 14th day of life were also the heaviest on the 66th day of life. King (9) comes to the conclusion that 11 albino rats maintained as a rule on the 150th day the same order as at birth, in respect to their body-weight. Analogical inferences can be drawn from the data collected by Gärtner (5) as to the monthly weights of 65 calves, during their first 6 months of life. My own calculations concerning the above material give the following coefficients of correlation between the birth-weight and the weight of growing animals in separate months: $+0{\cdot}530 \pm 0{\cdot}089$, $+0{\cdot}588 \pm 0{\cdot}081$, $+0{\cdot}422 \pm 0{\cdot}102$, $+0{\cdot}471 \pm 0{\cdot}097$, $+0{\cdot}510 \pm 0{\cdot}092$ and $+0{\cdot}497 \pm 0{\cdot}093$ respectively. The ratio of the coefficient to its probable error being always larger than the obligatory number 3, the above correlation may be regarded as biometrically significant[1].

The last volume of facts is of course of great importance for the

[1] The relation between the weight of calves at birth and the mature height at withers was studied by Eckles and Swett (4). The biometrical proof of the recorded data compels me to agree with these authors' opinion that little, if any, relation in this respect can be stated in Holsteins and Jerseys. Of comparable observations on birds only the investigations of Goldschmidt (6) referring to 21 Peking ducks are known to me. No relation between the weight of hatched ducklings and the weight of full-grown birds is found by this author.

problem of the morphogenetical value of the birth-weight in mammals. But, in all cases the animals had not ceased to grow before the observations were finished. Consequently the problem discussed is not entirely solved by the investigations quoted, especially as the authors mentioned have not considered separately the "external" and genetical agencies involved. Hence it follows that the conclusions drawn from the above data may require further verification. The following study is presented here as an attempt to solve these difficulties.

MATERIAL AND METHODS.

The material employed in my study consisted of 60 rabbits forming an F_2 generation from two Himalayan does sired by a Silver buck. The F_2 animals were obtained from 15 F_1 females, four years old when mated with their brothers. The food of the rabbits consisted of hay, oats, beets and boiled potatoes and was always administered with a certain excess. The F_2 young, born in the period from 5 May to 18 July, 1923, were supplied with fresh green stuff during the first three months of their lives. They were weaned at six weeks and helped through with goat milk. Six weeks later they were penned in separate cages. At the same time the supplementary feeding with goat milk was discontinued. The conditions of light, space and temperature in separate cages were made as uniform as possible.

As pointed out above, the age of F_1 females, as well as the quality and the quantity of food administered to each doe during the gestation period, was always identical. The only "external" factor, that could not be accurately controlled was the size of the different litters which is known to be negatively correlated with the weight of newly born rabbits. The duration of pregnancy being inversely correlated with the litter-size need not be considered separately here (cf. Kopeć (12))[1]. Only litters ranging from 4 to 9 young were taken into consideration. In order to rear the youngsters in possible uniform conditions from the very beginning, only 4 individuals were reared in every litter, all others being immediately killed. Exceptionally light or exceptionally heavy individuals, weighing less than 30 grm. or more than 60 grm. were all removed as I am convinced that the former die before maturity, while the latter

[1] The respective coefficient of correlation amounted to $-0{\cdot}586 \pm 0{\cdot}073$ in Himalayan does mated with a Himalayan or a Silver buck, being $-0{\cdot}421 \pm 0{\cdot}124$ in F_2 ex ♀ Himalayan × ♂ Silver. On the contrary, Hammond (8) in his most valuable monograph on reproduction in rabbits found no relation between the litter-size and the duration of the gestation period. As this author probably used in his studies material not genetically uniform the above discrepancy may be only apparent.

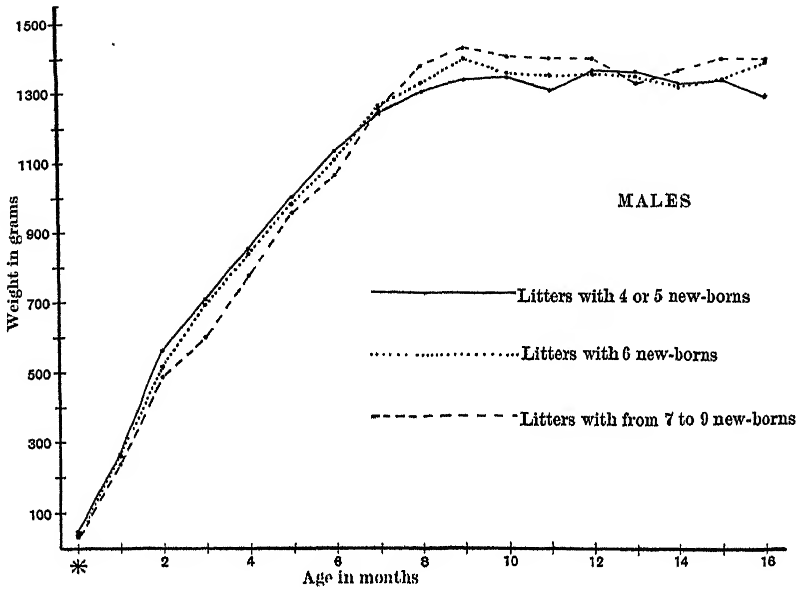
hinder the further development of their brothers in marked degree. As the number of such exceptionally heavy or light specimens was only 5 in the whole series, the general results cannot in any way be influenced by them. No other selection was made. I have further considered only such litters where the young did not die before weaning.

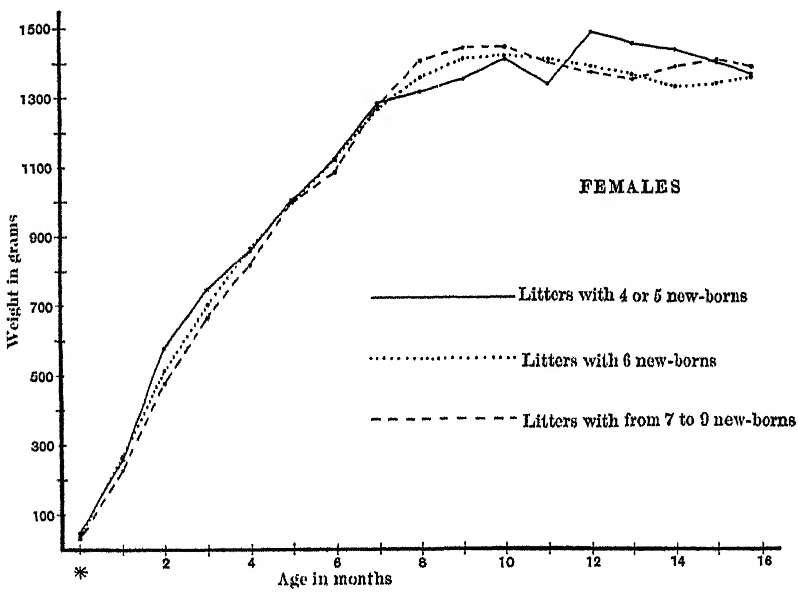
Thirty males and the same number of females were reared to maturity. None of them were sexually active during the time of observations. The newly born were always weighed before their first suckling, between the second to the sixth hour after birth (cf. Kopeć (10), p. 372). The weight of the growing rabbits was calculated for each month, from three weighings on successive days, made in the morning before feeding the animals: the last day of the preceding month and the first and second day referring to the month taken into consideration. Fragments of grams were considered as full grams except in the case of the new-born. The whole material of males and of females was twice segregated into special groups according to the litter-size or to the weight differences due to genetical factors (cf. below). In both cases the average weight of all animals of each discriminated group was determined and used for curves (Figs. 1–4). The observations lasted 16 months, *i.e.* much longer than the animals grew, growth being completed as a rule during the 9th and 10th month of the rabbits' life.

The Weight of Rabbits and the Birth-weight Differences due to Different Litter-sizes.

In order to ascertain whether and to what extent the weight of the growing and of the adult rabbit is influenced by the size of the litter I have divided the males and the females of my material into three groups according to the size of the respective litters. The groups were formed of litters ranging from 7 to 9, 6, and 4 to 5 young respectively. The average values for the groups amount to 8·4, 6·0 and 4·6 new-born for males and 8·3, 6·0 and 4·3 for females. The average weights of young at birth were 40·8, 42·3 and 45·9 grm. for males and 38·5, 42·7 and 48·6 grm. for females, a further proof of the negative correlation present between the size of a litter and the new-born's weight. In the corresponding groups 8, 9 and 13 males and 6, 17 and 7 females were examined.

The curves of Figs. 1 and 2 show that though the weight of the growing animals stands, in the beginning, as a rule in a direct proportion to its weight at birth, yet, starting from the 7th month in males and from the 4th in females, the regular increase mentioned becomes less noticeable. From the 8th till the 12th and from the 14th till the 16th month





Figs. 1 and 2. Curves of absolute growth of rabbits, in dependence on different litter-size. The day of birth is marked by an asterisk.

in males, as well as from the 8th till the 10th and from 15th till 16th in females, the former relation may be completely reversed, *i.e.* the lightest rabbits from the largest litters became the heaviest. Hence it follows that the differences of weight at birth, due to different litter-sizes, have no connection with the weight of the growing and full-grown rabbit. When looking through the items of Table I containing the monthly

TABLE I.

Monthly Coefficients of correlation between the litter-size and the weight of separate rabbits during growth.

Data referring to F_2 specimens ex ♀ Himalayan × ♂ Silver.

$r \pm E_r$, the coefficient with its probable error; r/E_r, ratio of the coefficient to its probable error; n, number of specimens.

	Males			Females		
Month	$r \pm E_r$	r/E_r	n	$r \pm E_r$	r/E_r	n
1	−0·443±0·099	4·5	30	−0·287±0·113	2·5	30
2	−0·373±0·106	3·5	,,	−0·301±0·112	2·7	,,
3	−0·506±0·092	5·5	,,	−0·329±0·110	3·0	,,
4	−0·275±0·114	2·4	,,	−0·068±0·123	0·6	,,
5	−0·126±0·121	1·0	,,	−0·116±0·121	1·0	,,
6	−0·295±0·112	2·6	,,	−0·155±0·120	1·3	,,
7	−0·094±0·122	0·8	,,	−0·086±0·122	0·7	,,
8	+0·154±0·120	1·3	,,	+0·060±0·123	0·5	,,
9	+0·224±0·117	1·9	,,	+0·060±0·123	0·5	,,
10	+0·092±0·122	0·8	,,	−0·052±0·123	0·4	,,
11	+0·138±0·121	1·1	,,	−0·010±0·123	0·1	,,
12	+0·045±0·123	0·4	,,	−0·244±0·116	2·1	,,
13	−0·135±0·121	1·1	,,	−0·238±0·116	2·1	,,
14	+0·072±0·123	0·6	,,	−0·192±0·119	1·6	,,
15	+0·130±0·121	1·1	,,	−0·048±0·123	0·4	,,
16	+0·162±0·120	1·4	,,	−0·068±0·123	0·6	,,

coefficients of correlation between the weight of each individual and the size of the litter, we may observe that the independence mentioned can also be demonstrated by biometrical methods. As the ratio of the coefficients to their probable error is here, as a rule, considerably smaller than the obligatory number 3, the correlation must be considered as fortuitous, especially as the sign of the coefficient was not in all cases negative.

Table II gives supplemental data for two litters derived from the same Himalayan doe sired by an Albino buck of unknown origin. The number of young in these litters was 3 and 8 respectively. Three young, all females, were reared in both these litters. From the recorded data it follows that, in these cases also, the negative correlation between the number of young in a litter and their initial weight is totally obscured after the 10th month of the rabbits' life.

TABLE II.

Average weight of rabbits during growth in grams in relation to the litter-size.

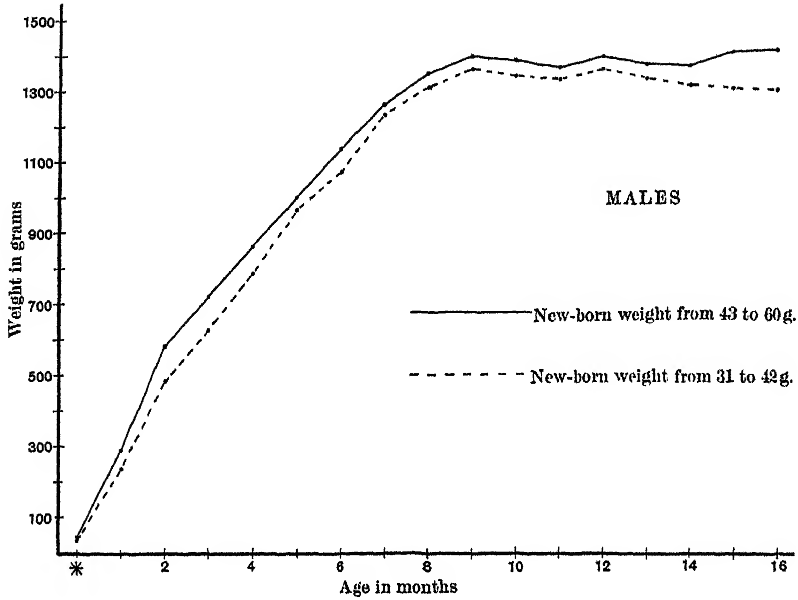
Data referring to females ex ♀ Himalayan × ♂ Albino.

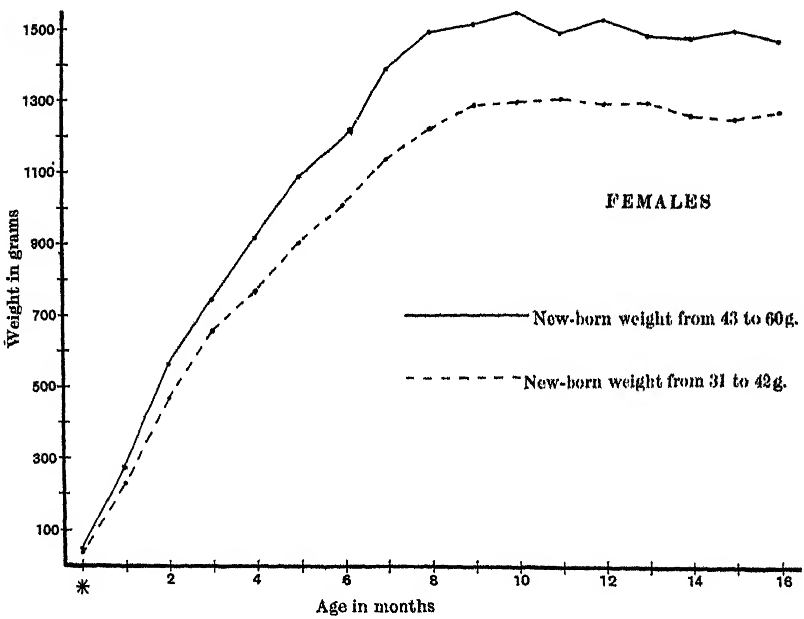
Month	Litter-size: Three new-borns	Litter-size: Eight new-borns	Month	Litter-size: Three new-borns	Litter-size: Eight new-borns
*	55·7	37·0	8	1609	1541
1	307	167	9	1798	1710
2	526	419	10	1854	1872
3	897	612	11	1970	2050
4	1069	909	12	2017	1931
5	1163	1012	13	1951	1976
6	1237	1221	14	1986	2026
7	1418	1338	15	1956	2053

THE WEIGHT OF RABBITS AND THE BIRTH-WEIGHT DIFFERENCES DUE TO GENETICAL FACTORS.

Quite different results were obtained when the genetics of the weight differences were taken into account. Dividing the newly born into two groups according to the new-born weight, regardless of the litter-size, we get two distinct groups, one ranging from 31 to 42 grm., the other from 43 to 60 grm. The averages for each group lie at 39·1 and 47·8 grm. for males and 36·4 and 49·3 grm. for females, the corresponding differences between both the groups amounting to 8·7 grm. in males and to 12·9 grm. in females. (The number of males examined was 15 in each group, of females 14 for the first and 16 for the second.)

The question arises now, whether the above differences have a genetical basis, or whether they are due to different sizes of litters in the two discriminated groups. (Other "external" agencies, which have an influence on the new-born weight being made uniform in this study, must not be considered here.) It should be at once admitted that the average size of the respective litters proved to be somewhat different for both groups. The average in the first group was 6·5 young per litter in both sexes. In the second the averages were 5·5 for males and 5·7 young per litter for females. It is therefore true that the litters differed in size in the two groups, but the corresponding differences did not amount to more than 1·0 young in males and 0·8 young in females. These small differences cannot be regarded as decisive, for the averages of the weight of the new-born in both groups are more strongly pronounced. The point discussed here is much better emphasised in the preceding chapter, where all the rabbits were divided into three groups in relation to the





Figs. 3 and 4. Curves of absolute growth of rabbits, in dependence on different genetical weight at birth. The day of birth is marked by an asterisk.

size of the litter regardless of the weight of the newly born. The differences in the average litter-size amounted there to 8·4 − 6·0 = 2·4 young in males and to 8·3 − 6·0 = 2·3 in females for groups 1 and 2, whilst they reached 6·0 − 4·6 = 1·4 for males and 6·0 − 4·3 = 1·7 in females on comparison of groups 2 and 3. On the contrary the average weight of the new-born did not differ more than 42·3 − 40·8 = 1·5 grm. for males and 42·7 − 38·5 = 4·2 grm. in females or 45·9 − 42·3 = 3·6 in males and 48·6 − 42·7 = 5·9 in females when comparing the groups 1 and 2 or 2 and 3 respectively. It follows therefore that when grouping the material as to the litter-size into three different classes, we find that relatively large differences in the number of young are connected with comparatively small differences in their body-weight at birth. Consequently, the distinct birth-weight differences noticed between both the groups in the present chapter must be atributed first of all to the action of genetic factors.

Figs. 3 and 4 show that rabbits weighing at birth genetically much, so to speak, maintain their higher values in comparison with the lighter newly born. The respective curves do not in any month meet together. The same conclusion must be drawn, when the corresponding data are studied by biometrical methods. The coefficients of the mentioned correlation being always positive are, as a rule, greater than three times their probable error (cf. Table III). Consequently, there cannot be any

TABLE III.

Monthly coefficients of correlation between the weight of new-born (dependent on genetical factors) and the weight of separate rabbits during growth.

Data referring to F_2 specimens ex ♀ Himalayan × ♂ Silver.

$r \pm E_r$, the coefficient with its probable error; r/E_r, ratio of the coefficient to its probable error; n, number of specimens.

	Males			Females		
Month	$r \pm E_r$	r/E_r	n	$r \pm E_r$	r/E_r	n
1	+0·662±0·069	9·6	30	+0·463±0·097	4·8	30
2	+0·538±0·088	6·1	,,	+0·536±0·088	6·1	,,
3	+0·520±0·090	5·8	,,	+0·576±0·082	7·0	,,
4	+0·469±0·096	4·9	,,	+0·498±0·093	5·4	,,
5	+0·333±0·109	3·1	,,	+0·571±0·083	6·9	,,
6	+0·420±0·101	4·2	,,	+0·588±0·081	7·3	,,
7	+0·361±0·107	3·4	,,	+0·597±0·079	7·6	,,
8	+0·363±0·107	3·4	,,	+0·598±0·079	7·6	,,
9	+0·259±0·115	2·3	,,	+0·377±0·106	3·6	,,
10	+0·299±0·112	2·7	,,	+0·447±0·099	4·5	,,
11	+0·296±0·112	2·6	,,	+0·270±0·114	2·4	,,
12	+0·330±0·110	3·0	,,	+0·545±0·087	6·3	,,
13	+0·322±0·110	2·9	,,	+0·565±0·084	6·7	,,
14	+0·383±0·105	3·6	,,	+0·665±0·069	9·6	,,
15	+0·544±0·087	6·3	,,	+0·683±0·066	10·3	,,
16	+0·592±0·080	7·4	,,	+0·715±0·060	11·9	,,

doubt as to the essential positive correlation between the "genetical" weight of the new-born and the weight of growing and of full-grown rabbits. The above correlation seems to be higher in females than in males. As the latter varied less at birth, the figures being 36–55 grm., than the former, which weighed at birth from 31 to 60 grm., it is very possible that various external life conditions more easily bring about greater uniformity in the less variable male.

Conclusions and Summary.

The above investigations suggest that though both external and genetic agencies affect the weight of new-born rabbits, only the latter have a distinct influence upon the weight of growing and adult animals. In other words, a definite morphogenetical value of the weight of the new-born was ascertained irrespectively of distinct modifications caused by the one variable present in the above inquiries, viz. the litter-size. Consequently, the "genetical" weight of the new-born being related to the weight of the animal when adult, furnishes a satisfactory method for the study of the inheritance of weight. Granting that the important environmental conditions of the growing foetuses, such as the age of the dam, her nutrition, the size of the litter, etc., are sufficiently uniform, the weights of the newly born give a satisfactory clue as to the weight of the future adult, and allow us to obtain results in genetical studies with a considerable gain in time and cost, as compared with the usual method of studying the weight of mature animals only.

It seems that a certain explanation should be given here in relation to my former results, referring to the inheritance of the weight of new-born rabbits (Kopeć (11)). Though the variability of the weight of the F_2 new-born is much greater than that of the F_1 animals of the ♀ Himalayan × ♂ Silver cross, the average values are about the same in both generations, that of the F_1 being intermediate between the new-born weights of both parental breeds. The greatest weight recorded for full-grown Himalayan females amounted, as stated in my paper, to 1831 grm. on the average, that for mature Silver does to 2286 grm. Consequently, if the new-born weight can be related to the adult weight, an average of about 2050 grm. in full-grown F_2 females of this cross should be expected. In contrast to such supposition, the average of the greatest adult weights reached by the F_2 females of this cross was in the present study not greater than 1423 grm. The fact, that in my previous genetical investigations only the heaviest does were used for the calculation of the average adult weight of the breed, chosen for further breed-

ing, and that records were taken also during the period of gestation, readily can account for the above apparent discrepancy. In the present paper all the F_2 females were recorded without any selection in respect of the weight. The common increase of females' bodies during the gestation as well as after the first parturition is well known. Stress must be laid, therefore, on the fact that the females of the present investigations had never been pregnant before. Consequently the disagreement between my present and former results is readily explained.

As pointed out elsewhere, there is no correlation between the size of the litter and the course of growth in rabbits (cf. Kopeć (13)[1]). On the contrary a remarkable connection was observed between the genetically determined birth-weight of a rabbit and its course of growth. The smaller the "genetical" weight at birth, the larger as a rule the per cent. increase of the body-weight, and smaller the absolute increase. I think, therefore, that, in studies of the course of growth, attention should be paid to the initial weight at birth, as differences in the course of growth due to genetic causes can be easily and unjustly attributed to special experimental conditions, and faulty conclusions drawn.

It seems that the morphogenetical value of the birth-weight may also be of some practical importance. Though no breeder can distinguish, at first sight, which variations of the initial body-weight are genetic and which environic in nature, yet the existence of genes, working throughout the growing period, should not be forgotten. For the selection of animals from separate litters the following rule most likely holds good: the greater the initial weight at birth, the greater the weight of the adult. Identical conclusions were drawn from the extensive studies of Benjamin (1). This writer, working with Leghorn fowls, proved a significant correlation between the size of growing and mature birds and the size of eggs from which the respective individuals hatched.

From the foregoing inquiries the following summary may be given:

(1) No connection exists between the birth-weight differences, due to the different litter-sizes and the weight of growing and adult rabbits. These birth-weight differences must be regarded as common modifications due to "external" conditions of the growing foetus.

(2) An essential positive correlation is stated between initial differ-

[1] Data referring to the sexual differences in weight are also given in the cited paper. A certain predominance of the weight of females over the weight of males, stated by Punnett and Bailey (15) and by Castle (2), was as a rule confirmed, also in these cases, when the rabbits were divided into separate groups according to the litter-size or to the genetical birth-weight differences.

ences in weight that have a genetic origin and the weight of growing and mature rabbits.

(3) On account of this morphogenetical value of the body-weight at birth the genetics of weight inheritance may be well studied on new-born mammals.

The above investigations were carried out in part by means provided by the Department of Science of the Ministry of Instruction.

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AN INHERITED ANOMALY OF DENTITION.

By O. A. BEADLE.

(With One Plate and One Text-figure.)

Hereditary defects of dentition are rare and it is believed that these observations have an interesting bearing upon the problem of heredity in man, especially when considered in connection with certain similar cases reported in the literature.

The purely genetical interest is therefore offered as an apology for presenting the results of investigations unavoidably lacking the completeness which would be demanded by an odontologist.

With the hope of increasing the value of this communication, the few relevant cases in the literature are discussed in connection with these original observations.

Such information as has not been directly confirmed and extended by personal examination of the patients, is believed to be perfectly reliable, though often rather desultory. It is to be regretted that no radiograms were obtainable.

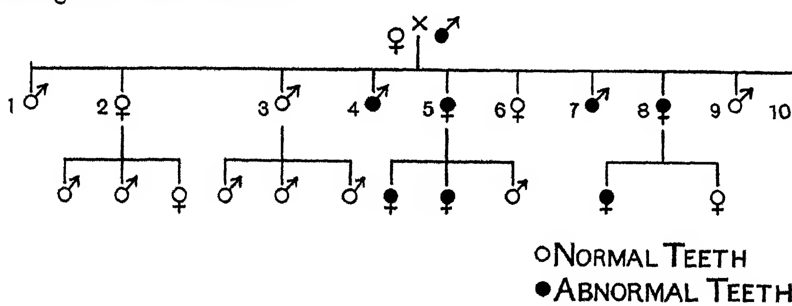

Fig. 1.

The essential anomaly in question is the sporadic absence of a varying number of teeth of both sets, which has been traced through three successive generations. There are also various irregularities in the age of eruption of the deciduous and permanent teeth.

The history begins with the two members of the parent generation (cf. Fig. 1). Of these the mother had normal teeth, but the father was deficient in certain teeth, the exact number not having been ascertained.

The F_1 generation consists of a family of ten, five of whom are de-

ficient in teeth in various ways. It has not been possible to examine many of these owing to their wide distribution over the globe. The ten children are as follows in order of age:

1. Male. Normal teeth; married but has no children.
2. Female. Normal teeth; married and has normal children.
3. Male. Normal teeth; married and has normal children.
4. Male. Abnormal dentition; died, no details forthcoming.
5. Female. Teeth abnormal; has three children, two of whom are deficient in teeth and one so far normal.
6. Female. Normal teeth; unmarried.
7. Male. Abnormal teeth; unmarried; not examined.
8. Female. Abnormal teeth; has two children, one of whom is deficient in teeth and the other normal.
9. Male. Normal teeth; unmarried.
10. Female. Abnormal teeth; unmarried.

Details of teeth deficiencies are not available except in a few cases which have been personally examined. This is so in the following, which includes both F_1 and F_2 generations.

1. 8th child: female. She lacks only the lower left central incisor. At the time of examination her two children were aged only three years and six weeks respectively, so it was too early to come to definite conclusions about the teeth; but the elder was almost certainly going to show abnormality of tooth development. The second, the mother thought, would be normal. These children are now six and three respectively and a recent letter states that the younger has the full complement of deciduous teeth, but that the elder has only sixteen teeth which are very widely spaced.

2. 5th child: female. She is very deficient in teeth and owing to the kindness of the Royal Dental Hospital, Leicester Square, I have been able to examine both her and her second child. Her dental formula is

	R.					L.	
0 0 0	1 0	1	0 1	1 0	1	0 0	1 1 1
0 0 1	1 1	1	0 0	0 0	1	1 0	0 0 0

The first child, a girl of 12 years old is also deficient in teeth. It is stated that she still has only her first set; but she has not been available for examination.

The second child, a girl of six years, has the following dental formula:

	R.					L.	
1	1 0	1	0 0	0 0	1	0 1	1
1	1 1	1	0 0	0 0	1	1 1	1

(Molars above and below the line are erupting.)

A photograph of her mouth was obtained.

The third child at the age of 12 months was normal; this is a male child.

3. 10th child: female. Lacks both lower central incisors and some back teeth, not determined.

In all these examinations allowance had to be made for extractions, and this was often difficult, but the above formulae are probably accurate in spite of this.

In many of these cases there has been great delay in the eruption of both deciduous and permanent teeth; this is markedly so in the eldest child of No. 5. Further, it should be noted that often the mother has been led to suspect the existence of an abnormality before the teeth have all appeared, from the spacing of the teeth and form of the jaw. In some cases, where the first set was deficient, the gaps were filled by the permanent teeth, but nevertheless gaps always remained in some places among the latter.

Particular attention is drawn to the following points:

(1) The abnormal dentition seems to behave perfectly as a Mendelian dominant, this dominant factor being present in the heterozygous state in the male parent. The F_1 offspring show 50 per cent. of the dominant abnormal and 50 per cent. of the recessive normal characteristic; further, in the two families of F_2 offspring examined and described above it is tempting to believe that a similar ratio has occurred, as expected, in spite of the small size of those families.

(2) Although pains have been taken where possible to find the exact nature of the tooth abnormality, the failure to do this in so many of the cases does not rob the observations of all their interest, since the most striking feature of the whole series, besides the regularity of inheritance according to Mendelian laws, is the great irregularity of the deformity itself. Any of the teeth may be affected as far as the data available indicate, except the canines.

(3) At the outset of the investigations a correlation was suspected

between tooth deficiency and dark hair colour. It was found however that there are three exceptions to this rule. In spite of this there is a very striking parallelism, at least fifteen cases conforming to the rule against the three exceptions. The father, four of the abnormal children (the fifth being fair), and all the abnormal grandchildren except one are dark, while all the rest of the family are fair; except one of the normals who is dark (2nd child of 8). Are we perhaps dealing with a case of linkage between two genes with a crossing-over value of about 10 per cent. in the male? The number of cases is insufficient to make this more than suggestive.

Discussion.

Although a Wassermann test has not been obtained in any of these cases, it is almost certainly not merely a case of transmitted syphilis; there is nothing to make one suspicious of this disease; the family is generally speaking a healthy one; moreover, absence of teeth due to congenital syphilis is apparently not reported. We are certainly dealing with a true hereditary factor. Is this an inherited general physiological abnormality of which the dental defect is only a part? Unfortunately there are no means of testing this. A history of idiopathic tetany or convulsions would have been interesting as suggesting some defect of calcium metabolism; but nothing of this kind is present. It seems more likely that we are dealing with a true genetic factor, a change or mutation, perhaps, in some gene which exerts its effect on the tooth germ itself, quite apart from any inherited general anomaly in the body as a whole.

This view is made still more probable when considered together with the extremely careful series of observations recently published by Wheelon. These cases all have reference to the lateral incisors only, which are apparently the most frequently missing of any teeth.

The three first cases show definite hereditary defects of the upper lateral incisors, transmitted through the female line in each instance. Case II is a patient with a congenitally absent right upper lateral incisor. The mother, maternal grandmother, three sisters, two brothers and a nephew all show a similar defect. Case III lacked the upper lateral incisors. A similar defect was possessed by the mother, maternal grandmother, four maternal aunts, one maternal uncle, one sister and this sister's daughter, *i.e.* four generations. Wheelon's cases all show various hereditary general disorders such as extreme nervousness, diabetes, menstrual disorders, etc.; but none of these showed a parallelism

with the tooth defects. He tries to bring all the patients described under the head of dyspituitarism, but the evidence given for this does not seem very convincing, and there does not seem more justification for explaining the tooth deficiencies as part of a general metabolic disturbance than in our own cases.

There is a greater uniformity among Wheelon's cases than our own, although there are variations; for instance, in Case II, where the rule is the absence of the right upper lateral incisor, one sister lacked the left upper lateral incisor. Again in Case III, which lacked usually both upper lateral incisors, one maternal aunt was minus a right upper lateral incisor and a sister with her daughter a left upper lateral incisor.

Our case is very irregular and is the only case so far discovered in the literature which involves the molars as well as the incisors. According to Pitts the third molar and lateral incisors are the most frequently absent of all the teeth.

Now this irregularity is in striking contrast to a further series of cases described.

The most instructive of these is that of Thadani, who describes a hereditary absence of all teeth in a race living in India. The toothless members, who are called Bhudas, are all males and transmit the defect through the female line only; in fact it is a case of ordinary sex-linked inheritance. Incidentally the toothlessness is associated with baldness and sensitiveness to heat.

Ovazza, again, reports in two families the hereditary absence of all incisors, behaving as a single dominant Mendelian character. This case is similar in genetic behaviour to ours, but unlike ours, is constant.

We would submit, therefore, that there are three types of congenital tooth defects.

I. Absence due to malnutrition after, or shortly before, birth and not inherited: *e.g.* Wheelon's fourth case. A good example of this is one given by Hopson, a Ghond with complete absence of both deciduous and permanent teeth, probably due to extreme malnutrition; there was no hereditary history. This may occur also in more than one member of the same generation of a family, probably through the same influences acting on all the members concerned, perhaps *in utero*. An example of this is a case of Pitts' of two brothers, both having an absence of deciduous and permanent central incisors and also of permanent lateral incisors.

These cases must not be confused, however, with true hereditary defects.

II. Inherited, but inconstant tooth defects; such are our own case and Wheelon's first three cases.

III. Inherited and very constant tooth defects behaving exactly like any other Mendelian characters. Such are Ovazza's and Thadani's cases.

These last two types of inherited characters suggest certain considerations with regard to the nature of the hereditary unit, which are briefly discussed here.

The striking parallelism between the distribution of chromosomes among the progeny of a pair of individuals and that of certain morphological or physiological characteristics has given rise to the most fruitful conception of the gene.

Now it has hardly been sufficiently emphasised that the recognition in the first instance of the Mendelian unit, as a concrete entity depended upon two important conditions which are by no means always satisfied.

(1) In an often complex combination of morphological differences inherited together as a single unit, there is sometimes one which meets the eye at once and gives the unit its name (eye colour, abnormal wings, etc.), but this is usually only part of a complex whole.

(2) In spite of the existence of segregation and recombination of other units not under observation, in accordance with Mendel's Second Law, there are many unit characters of such potency that they retain their distinctive form unchanged.

These facts enabled the idea of the hereditary unit as a thing of constant value and calculable history to be evolved.

After this had been grasped and Mendel's Second Law was established it was shown that many characters superficially of a like kind, though not inherited as a single unit, but apparently unstable, could be explained as the result of the mutual influence of two or more pairs of units upon one another, each pair however being distributed by exactly the same mechanism as the single pair of characters first studied.

But the recognition of this single unit would have been prevented, or at any rate delayed, were it not for the development by some such units of so great a potency that they determine certain salient characters, as part of a whole which is ignored, and moreover are not at the mercy of influences from other units associated with them in all sorts of combinations as a result of Mendel's Law of independent assortment.

Briefly stated, a single gene often determines characters which are constant in visible form in spite of the various permutations and combinations of other genes with which it coexists.

This suggests the idea of a variable ascendancy of some genes over the potential influence of coexisting genes. Potency of this kind might, of course, involve only one definite element of the complex of characters it determines. Now a change in a gene could have little evolutionary value until it had become potent enough over other genes to maintain a stable change in some one morphological or physiological character.

There is a further type of stability needed, namely an ability to resist modification in the interaction with environmental influences during embryonic development.

That such modification occurs we know from the famous experiments of Morgan on *Drosophila melanogaster*, in which the physical condition of the culture medium greatly changed the end result of certain genes.

The value of a change in a given locus in a chromosome will depend, then, partly upon its potency to maintain a stable change in some structural character regardless of the two influences tending to make it inconstant:

(*a*) Its genetic environment as we might express it, *i.e.* the associated genes which in various combinations are tending to modify its result.

(*b*) The subtle, incalculable influences of environment with which it co-operates to produce its end result.

These theoretical considerations are given because it is believed that the foregoing observations of tooth anomalies help to lend them interest.

It is suggested that we see here two degrees of stability of the hereditary unit.

In our own cases we are certainly dealing with a change in a single gene which is severely influenced by indeterminable changes either in general genetic constitution or in environmental interaction, or both; we cannot say which is the predominant factor.

In the cases of Thadani and Ovazza quoted, however, the change has sufficient inherent potency to give a constant result even in spite of the varying conditions under which it is placed. It is changes of this type, we would urge, that alone can have any importance for the theory of evolution by Mutation. If it is objected that we are dealing merely with a transmitted "weakness of the germ plasm," as has been argued in the experiments of Stockard and others on the inherited effects of poisons, the answer is that a "weakness" is only a change in a factor whose result is possibly or actually detrimental to the organism. Surely such a weakness might equally well be the origin of a useful character, in which case it would need only a sufficient stability in the face of almost overwhelming modifying forces, to be of evolutionary significance.

If these armchair speculations, appended to such slender observational data, need an apology, this must be that they are based upon the enormous mass of experimental results which has been collected in recent years by the brilliant researches of Morgan and the galaxy of other investigators who owe their inspiration to him.

Acknowledgment is gratefully made to those friends whose assistance in various directions has enabled this paper to be got together; in particular to Prof. J. S. Huxley at whose suggestion the enquiry into this family history was undertaken.

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EXPLANATION OF PLATE XVI.

Views of dentition of upper and under jaws of second daughter of ♀ No. 5 in pedigree.

PLATE XVI

DOMINANT BLACK IN CATS AND ITS BEARING ON THE QUESTION OF THE TORTOISESHELL MALES.

By K. TJEBBES and CHR. WRIEDT.

The existence of two different kinds of black colour in cats was indicated in Tjebbes' experiments on Siamese cats, published in 1924.

A mating reported between Siamese and tabby (wild type) gave 3 blacks. Three other Siamese × tabby matings, not yet published, have also given black heterozygotes only, together 10 uniformly black-coloured young.

In F_2 from these black cats came 4 blacks, 1 tabby and 2 Siamese. These Siamese are genetically blacks, for from other data Tjebbes has shown, that tabby may be combined with the recessive factor that causes the Siamese pattern.

One of the F_2 Siamese was mated with one of the black F_1 males; the result was 1 black, 1 Siamese, 1 tabby. These matings thus gave together 8 blacks (uniform blacks plus Siamese) against 2 tabbies. No doubt these data are scanty, but when we remember that different factors for black colour, the one dominant over wild type and the other recessive, now have been found in rabbits, dogs and swine, we do not hesitate to contend that in cats also two such factors may be present.

In *rabbits* Punnett in his well-known paper of 1912 proved the existence of dominant black. It is not without interest to mention that this factor was detected in a member of the albino series, viz. the acromelanistic Himalayan rabbit, the nearest parallel to the Siamese cats.

In *dogs* Treschow has published a note on matings between black Norwegian deerhounds, that have given together 23 blacks and 5 wild type colour (grey with banded hairs). These results combined with the fact that wild colour × wild colour has never given black in the Norwegian deerhound, show clearly that we here have a black that is dominant over wild type. The occurrence of recessive black in dogs is proved by different investigators, recently by Anker in dachshund. The wild type is here completely dominant over the black of the black-and-tans. Further, Wriedt is in possession of unpublished experimental data confirming Anker's conclusions.

With regard to *swine* Nachtsheim has obtained data, so far as we know not yet published, showing that the German breed "Hannoveranisches unveredeltes Landschwein" has a homogeneous black that is dominant over wild type; but in Berkshire pigs the same author has stated that the black colour is recessive to wild type.

The occurrence of this dominant black in cats is of a special interest as it, according to new experiments of Tjebbes, has a bearing on the often discussed tortoiseshell males.

In a new series of experiments with Siamese cats Tjebbes mated a Siamese female with a striped yellow male. This mating has given three young, all tortoiseshell, and two of them were males.

All earlier workers on tortoiseshell cats agree upon the extreme rarity of tortoiseshell males. According to Doncaster only three amongst 225 males from matings black × yellow, tortoiseshell × yellow, and tortoiseshell × black, were tortoiseshell-coloured Those few males have caused considerable mental exercise to geneticists. It has been a general belief, that tortoiseshell males are infertile and this supposed sterility has caused different authors to put forth hypotheses in order to account for their occurrence (Doncaster, Little, Bonnevie). So it has been supposed, that the tortoiseshell male is either a non-disjunction, or a case parallel to the free-martin in cattle. But Doncaster has mentioned that cat-breeders have had offspring from such males.

In the light of the fact above related, that two tortoiseshell males were produced by a mating of dominant black × yellow, we think it is more probable that even in the other rare cases known in literature the cooperation of dominant black with yellow is the cause of the exceptionally produced tortoiseshell tom-cats.

As to chromosomes it is of course not yet possible to give a full explanation, but we wish to call attention to Aida's and Winge's results, that genes may be found in the Y-chromosomes of vertebrates. This, and the circumstance that sex-linked inheritance in mammals has been found in only three cases, makes it very probable that sex-linked inheritance is often masked by the lying of genes in the Y-chromosome; also that crossing-over between the X- and the Y-chromosome may take place. Something of this kind may perhaps occur also in our case.

Further experiments on these questions are going on and will be published in process of time.

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ON THE TOPOGRAPHY OF THE SEX-CHROMOSOME IN FOWLS[1].

By A. S. SEREBROVSKY and E. T. WASSINA.

At the Anikowo Genetical Station is carried on the study of the sex-chromosome in fowls, and the phenomena of crossing-over between sex-linked characters in fowls[2] had already been observed in 1922.

Later on, by a set of special matings and an exact record of all cases of cross-over, we endeavoured to find the relative distribution of these genes in their chromosome, and to determine the distance between them, having in view the construction of a map of the sex-chromosome of fowls.

We studied the following genes (in the order of their location) *Trage*, *Trufege*, *Tuge*, *Suke*.

(1) *Trage*-gene (Tg; its absence tg = *atrage*), causing the well-known pattern of Plymouth Rock colouring. This character is easily determined at the early age of 1–2 days in the Plymouth Rock colouring, that is to say in the presence of *Tifa* (melanism). In most other combinations *Trage* appears at an older age, *i.e.* at 1½–2 months. And some forms of *Trage* are so difficult to establish, that to decide whether it is present or absent is only possible after having observed the progeny of the doubtful bird. Such difficulties, as we have pointed out, do not always allow the use of the whole of our material.

(2) *Trufege* (Tfg; its absence tfg = *atrufege*), the gene of yellow legs characteristic of some races of fowl: Indian game, Orloffs and others.

Unfortunately, till now, we have not always succeeded in establishing the presence of this gene with complete certainty.

First of all the colour of the legs is definitely determined at about three months old, at which age, if not earlier, a considerable number of chickens perish. Moreover the presence of certain colour characters ("buff," *Tofa*-gene) (melanism, *Tifa*-gene) and the presence of negro-pigment (*Trule*-gene), influence the leg-colouring, hindering the normal manifestation of the *Trufege* gene.

(3) *Tuge* (Tu; its absence tu = *atuge*), silver (white) colouring or marks, well-known in fowls; often described in English literature (Haldane, Davenport, Sturtevant, Punnett), called "silver" (S). Unfortunately it is very difficult to establish the presence of "silver" when

[1] From the Anikowo Genetical Station, Director Prof. N. K. Koltzoff.

[2] Serebrovsky, A. S., *The American Naturalist*, LII. Nov.–Dec. 1922.

the *Tifa*-gene (melanism) is present. In such cases it is most convenient to observe *Trage*.

(4) *Suke* (S; its absence s = *asuke*), the inhibitor of the rate of feathering in chicks, a very convenient character thanks to its appearance at an early age and the ease with which it is determined[1].

Suke chicks, when one month old, still have the wings little developed and very short tails. The *Suke* chickens on the tenth day of their birth differ most sharply from the *asuke*. Hence this gene can be recorded at this age, thus affording the possibility of making use of nearly the whole material.

As we have said, it is hardly possible to observe simultaneously the heredity of all four genes. It is easy to observe the pairs *Trage-Suke*, more difficult *Tuge-Suke*, much more difficult *Trage-Trufege*, *Trage-Tuge*, and even more so to study three simultaneously. Later on it will be necessary to create forms with such combinations of genes, as to enable us to establish at an early age the presence or absence of all the genes studied.

In the present report we have made use only of chickens, in which the presence or absence of the genes under consideration was definitely established.

To determine all the types of crossing-over, there have been carried out investigations on pairs of the genes studied.

(1) *Trage-Trufege*.

The gene of yellow legs is, evidently, located close to the gene of the cross-barring pattern *Trage*-gene. Hitherto we have not noticed a single case in which these two characters broke apart.

Out of 69 chicks in this test, only two cases are marked as crossovers with a note of interrogation. One of these *trage-atrufege*, and the other *atrage-trufege*. In both cases the colouring of the legs is doubtful. Both chickens perished, therefore we did not succeed in determining exactly this colouring (Table I).

TABLE I.

Crossing-over between Trage *and* Trufege.

	$♂♂ \frac{Tg\ Tfg}{tg\ tfg} \times ♀♀ \frac{tg\ tfg}{—}$		Total
Trage Trufege	29	67 non-crossovers	67 non-crossovers
atrage atrufege	38		
Trage atrufege	1	2 crossovers (?)	2 crossovers (?)
atrage Trufege	1		

[1] See Warren, *Journal of Heredity*, 1925.

All the ♂♂ investigated had the structure $\frac{\text{Tg Tfg}}{\text{tg tfg}}$, and fowls mated with them had the structure $\frac{\text{tg tfg}}{\text{—}}$ and some $\frac{\text{tg Tfg}}{\text{—}}$. Of the offspring of the latter only the ♀♀ were counted.

(2) *Trage-Tuge.*

The breaking apart of these two characters was observed rather often. Out of 77 chicks recorded we got 33 cases of crossing-over, *i.e.* 43 per cent. ± 5·60 per cent.[1]

There were investigated both couplings between Tg and Tu in structure $\frac{\text{Tg Tu}}{\text{tg tu}}$ and also repulsion in structure $\frac{\text{Tg tu}}{\text{tg Tu}}$. But repulsion between Tg and Tu, all cases of their reunion and *vice versa* of the simultaneous absence of both in their progeny are cases of crossing-over (Table II).

TABLE II.

Crossing-over between Trage *and* Tuge.

	♂♂ $\frac{\text{Tg Tu}}{\text{tg tu}}$ × ♀♀ $\frac{\text{tg tu}}{\text{—}}$		♂ $\frac{\text{Tg tu}}{\text{tg Tu}}$ × ♀♀ $\frac{\text{tg tu}}{\text{—}}$		Total
Trage Tuge	21	35 non-crossovers	4	8 crossovers	44 non-crossovers
atrage atuge	14		4		
Trage atuge	13	25 crossovers	6	9 non-crossovers	33 crossovers
atrage Tuge	12		3		43 % ± 5·60 %

The linkage between "silver" and "cross-barring" of the Plymouth Rock pattern was studied by Haldane[2]. In 1921 he described 35 per cent. of crossing-overs as having appeared in his experiments. Agar[3] recorded 35·7 per cent. crossing-overs in Wyandotte × Plymouth Rock matings and 46·4 per cent. in Rhode-Island matings.

(3) *Trage-Suke.*

Suke is located from *Trage* at about the same distance as *Tuge*. Out of 189 chickens, crossing-over occurred in 83 cases; *i.e.* 44·0 per cent. ± 3·6 per cent. of crossing-overs (Table III).

[1] The error has been calculated according to formula $m = \frac{\sqrt{p\,\%\, q\,\%}}{n}$.

[2] *Science*, Dec. 30, 1921.

[3] *Journal of Genetics*, XIV, 1924, p. 265.

TABLE III.

Crossing-over between Trage *and* Suke.

	$♂♂ \frac{Tg\ S}{tg\ s} \times ♀♀ \frac{tg\ s}{—}$		Total
Trage Suke	54	106 non-crossovers	44 % ± 3·6 %
atrage asuke	52		
Trage asuke	43	83 crossovers	"
atrage Suke	40		

(4) *Trufege-Suke.*

The distance between *Trufege* and *Suke* is very great. Crossing-overs occurred in nearly half of the cases—49·0 per cent. ± 5·9 per cent. (Table IV).

TABLE IV.

Crossing-over between Trufege *and* Suke.

	$♂ \frac{Tfg\ S}{tfg\ s} \times ♀♀ \frac{tfg\ s}{—}$		Total
Trufege Suke	14	36 non-crossovers	49 % ± 5·9 %
atrufege asuke	22		
Trufege asuke	20	34 crossovers	"
atrufege Suke	14		

(5) *Tuge-Suke.*

These two genes are in the following relation: out of 112 chickens, we recorded 21 cases of crossovers, which makes—19·0 per cent. ± 3·7 per cent. (Table V).

TABLE V.

Crossing-over between Tuge *and* Suke.

	$♂♂ \frac{Tu\ S}{tu\ s} \times ♀ \frac{tu\ s}{—}$		$♂♂ \frac{Tu\ s}{tu\ S} \times ♀♀ \frac{tu\ s}{—}$		Total
Tuge Suke	44	72 non-crossovers	3	4 crossovers	91 non-crossovers
atuge asuke	28		1		
Tuge asuke	10	17 crossovers	10	19 non-crossovers	21 crossovers
uge Suke	7		9		19 % ± 3·7 %

From these data we can arrange the four genes in the following approximate order: *Trage* with *Trufege* located close to it at one end of the chromosome, and *Tuge* with *Suke* at the opposite one.

Since the percentage of crossing-overs shown by the pair *Trage-Suke* (44·0 per cent. ± 3·6 per cent.) and by the pair *Trage-Tuge* (43·0 per cent. ± 5·6 per cent.) is nearly the same, we cannot say which of

the two, *Tuge* or *Suke*, is the next to *Trage*. We suggest the order: Tg, Tfg, Tu, S, partly from our earlier data of a few years ago (see Serebrovsky, 1922), and partly on the basis of Haldane's data, who obtained between Tg and Tu 35 per cent. of crossing-overs. We must suppose that the distance between the two loci is great, for the real percentage of crossovers is greater than the observed owing to double crossing-overs which cannot always be detected. That the double crossing-over occurs is obvious from the cases where, between two genes, a third one is located, which gives a crossing-over with both extreme genes.

In our material we had two cases of double crossing-overs (see Tables VI and VII).

TABLE VI.

The double crossing-overs.

$$♂♂ \frac{\text{Tg Tu S}}{\text{tg tu s}} \times ♀♀ \frac{\text{tg tu s}}{—}$$

Non-crossover		Crossover 1		Crossover 2		Crossover 1, 2		
Tg Tu S	tg tu s	Tg Tu s	tg tu S	Tg tu s	tg Tu S	tg Tu s	Tg tu S	
9	3	1	1	5	6	0	1	In the 26 cases 1 double crossover

TABLE VII.

The double crossing-overs.

$$♂ \frac{\text{Tg tu S}}{\text{tg Tu s}} \times ♀♀ \frac{\text{tg tu s}}{—}$$

Non-crossover		Crossover 1		Crossover 2		Crossover 1, 2		
Tg tu S	tg Tu s	tg Tu S	Tg tu s	tg tu S	Tg Tu s	Tg Tu S	tg tu s	
6	3	0	0	3	4	0	1	In the 17 cases 1 double crossover

We hope to solve the problem before us, viz. the working-out of a map of the sex-chromosome—by further accumulation of material; but for this we must, however, find a new gene, located between Tg and Tu, to help us to determine the exact distance and order between the sex-linked genes. Such a gene may turn out to be *Trama*, described under symbol S (= Spangling) by Lefevre and Rucker[1], and now being studied at the Anikowo Genetical Station.

[1] *Genetics*, VIII, 1923 . 367.

The study of the sex-chromosome of fowls, apart from its theoretical importance, is of great economic interest, for Pearl and Surface have described an intensifier of egg-laying, located in the sex-chromosome.

Since work of this nature was started at the Anikowo Genetical Station, this question has formed part of our programme of investigation. In the progeny of a Pavloff cock, in which segregation occurs in relation to gene *Tuge*, were compared the egg-laying of *Tuge* and *atuge* sisters, but the recorded data are still difficult to interpret[1].

At the present time at the Anikowo Genetical Station are carried on further experiments on investigation of the rôle of different areas of sex-chromosome on transmission through inheritance of elements of egg-laying. A. N. Promptov studied 23 cocks of our flock to test the presence of lethal genes in the sex-chromosome. In spite of considerable variations in the sex-ratio in the offspring of some cocks, no lethal genes were found.

[1] See A. S. and R. I. Serebrovsky in "Genetics of Domestic Fowls," *Transact. of the Anikowo Genetical Station* (in the press).

NOTE ON A CHINCHILLA-JAPANESE CROSS IN RABBITS.

By R. C. PUNNETT, F.R.S.

(With One Text-figure.)

Introduction. Some experimental results obtained from the Japanese rabbit by Professor Castle and by myself[1] led us independently to the conclusion that the "Japanese" pattern could be regarded as a member of an allelomorphic series in which the other known terms are yellow[2], recessive black, and dominant black. On this view of the genetical nature of the Japanese pattern it is assumed that the yellow there found associated with black is identical with the yellow of the various forms of yellow rabbits. It occurred to me that this assumption might readily be tested by examining the results of a cross between the Japanese and the chinchilla rabbit. Several years ago Castle showed that the chinchilla of the fancy may be regarded as an ordinary agouti from which the yellow colour is almost or quite absent. Where the banded hairs of an agouti are yellow they become silvery in the chinchilla, which perhaps ought more properly to be termed a silver agouti. The difference between an agouti and a chinchilla lies in the almost complete absence of the yellow, the melanic pigment being apparently unaffected. In the course of his work Castle "chinchillated" the yellow rabbit in the agouti series, which frequently contains little more than a trace of melanic pigment, and he found that such animals were almost pure white with the bluish smoky eye of the chinchilla[3]. Now if the yellow of the Japanese is of the same nature as the yellow of ordinary yellow rabbits we ought to be able to obtain from a cross between the chinchilla and the Japanese a form of the latter in which the black markings are on a white instead of on a yellow ground.

Experimental Data. A chinchilla doe (S 158) was obtained from a well-known breeder and mated at different times to two Japanese bucks of which one (S 68) was heterozygous for the agouti factor, while the

[1] *Journ. Genetics*, XIV. pp. 225–240.

[2] "Yellow" here is a general term comprising tortoise (=sooty yellow) as well as the yellow that contains the agouti factor.

[3] *Journ. Heredity*, XV. 1924.

other (S 163) lacked it. As shown in the subjoined pedigree, she gave with the former buck 7 agoutis and 2 blacks, while from the other she produced 5 agoutis and 5 blacks, showing her to have been heterozygous for agouti.

♂ S 68 × ♀ S 158 × ♂ S 163

7 agouti viz. ♂ S 174, ♀ S 180, ♀ S 181, ♀ S 182, ♀ S 183, ♀ S 184 and another

2 black viz. ♂ S 175 and another

5 agouti

5 black viz. ♀ S 230, ♀ S 231, ♀ S 232, ♀ S 233 and another

The 5 agouti F_1 does (S 180–184) were all mated with the black F_1 ♂ S 175 to produce an F_2 generation, while three of them (S 182–184) were also mated with the agouti F_1 ♂ S 174. The results obtained are shown in Table I.

TABLE I.

	Agouti	Chin.-Ag.	Black	Chin.-black	Japanese	Wh. Jap.
♀ 180 × ♂ 175 (black)	6	2	4	2	4	—
♀ 181 × ”	10	4	—	—	1	2
♀ 182 × ”	3	1	2	1	—	—
♀ 183 × ”	1	—	6	1	2	—
♀ 184 × ”	4	4	4	—	3	2
	24	11	16	4	10	4
♀ 182 × ♂ 174 (ag.)	6	—	4	—	4	—
♀ 183 × ”	4	1	—	1	1	—
♀ 184 × ”	4	2	—	—	—	—
	14	3	4	1	5	—

As the table shows, six colour classes made their appearance, viz. the three classes agouti, black, and Japanese, together with the three corresponding forms in the chinchilla series. Of these the Japanese chinchilla was the most striking, and, as had been anticipated, was an animal with the characteristic black markings of the Japanese, but on a white instead of on a yellow ground (cf. Fig. 1).

The appearance of such animals leaves little doubt that the yellow of the Japanese rabbit is identical with that of the ordinary yellow rabbit.

The data in Table I also seem to show that the relation between the yellow-white, and the self-Japanese pairs of characters is a simple Mendelian one, *i.e.* that linkage does not enter into it. From this point of view the figures may be summarised as follows:

		Exp.
Yellow selfs (agoutis + blacks)	58	**54**
White selfs (chin.-agouti + chin.-blacks)	19	**18**
Yellow Japanese	15	**18**
White Japanese	4	**6**

There is a slight deficiency in the Japanese classes but the figures are sufficiently close to a 9 : 3 : 3 : 1 ratio to preclude the likelihood of any linkage between the characters concerned.

Fig. 1. White Japanese rabbit. From a photograph by M. S. Pease.

This view is confirmed by the results of a back cross made by mating the 4 black F_1 ♀♀ (S 230–233) with a white Japanese F_2 buck (S 187) as shown in Table II:

TABLE II.

	Agouti	Chin.-ag.	Black	Chin. black	Japanese	White Jap.
♀ 230 × ♂ 187	1	2	—	1	2	—
♀ 231 × ,,	—	1	2	1	2	—
♀ 232 × ,,	—	1	2	—	3	3
♀ 233 × ,,	—	—	—	—	3	3
	1	4	4	1	10	6
Exp.	**3·4**	**3·4**	**3·4**	**3·4**	**6·8**	**6·8**

The expected six classes appeared and, having regard to the paucity of numbers, in proportions not far removed from those expected.

We may conclude then (1) that the yellow of the Japanese is identical

with the yellow of other rabbits, and (2) that there is no linkage between the yellow-white and the self-Japanese pairs of characters.

In conclusion, the chinchilla-black which appeared in these experiments calls for a few remarks. In coat colour this form was indistinguishable from an ordinary black. It was however recognised as belonging to the chinchilla series by its eye colour which, as development proceeded, showed the smoky blue tint characteristic of chinchillas in the black series (*i.e.* as opposed to chocolates) instead of the rich brown of a normal black. That the chinchilla-black is not necessarily of this type is clear from a recent publication of Castle[1] where he describes a form as in pigmentation "less heavy than that of an ordinary non-agouti black rabbit becoming in most parts of the body a dull, faded, brownish-black," though at the same time "the more intensely pigmented extremities may be described as black." In the same paper Castle also distinguishes between two forms of chinchilla-agouti, viz. a darker and a paler which he regards as allelomorphic to one another. It is clear from his work, as he points out, that the chinchilla form of black, or "sepia," bred by him corresponds to the paler type of chinchilla-agouti. The chinchilla-blacks that came in my experiments doubtless correspond to the darker type of chinchilla-agouti. Though variable in shade they were at about 10 days old much closer to the ordinary agouti than to the young pale type shown by Castle on Plate 3, fig. 1 *b*. Further, they often, though not always, showed some tinge of yellow in their first coat, especially on the back, a feature which Castle states is not found in the paler type, and is regarded by him as diagnostic of the darker.

I may add that this tinge of yellow in the baby coat is sometimes to be found in white Japanese, and in the case of one F_2 ♂ (viz. S 213, ex ♀ S 181 × ♂ S 175) it was so marked that the animal was reared and mated back to the original chinchilla ♀ (S 158). Since he gave nothing but chinchilla young, 8 in all, there can be no doubt that he was a white Japanese. In this case the yellow tinge persisted after the baby coat was moulted, though it had nearly disappeared at the age of one year.

The cost of the experiments of which an account is given above was for the most part met by grants from the Government Grant Committee.

[1] Publ. No. 337 of the Carnegie Institution of Washington, 1926.

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LINKAGE AND INDEPENDENT INHERITANCE IN *PISUM SATIVUM*.

BY ASLAUG SVERDRUP.

(*Student of the John Innes Horticultural Institution.*)

(With Two Plates (one in Colour) and Five Text-figures.)

CONTENTS.

THE present investigation was started in 1919 by C. Pellew and W. Bateson for the purpose of testing on a big scale the interrelationship of Mendelian factors in *Pisum*. The first results were published in 1923 (Pellew and Sverdrup) when a short account was given concerning the inheritance of yellow pod together with some new linkages. The work has since been carried on, and several more factors have been brought into the experiment. I am greatly indebted to Miss D. de Winton for her valuable help which enabled me to carry out the experiments on a much larger scale than would otherwise have been possible. The cytological preparations of the material were made by Mr W. C. F. Newton.

MATERIAL.

The following account deals with fifteen pairs of factors all of which show a monofactorial segregation. Some care has been taken in selecting characters easily distinguishable in homozygotic as well as heterozygotic condition in order to avoid uncertain results caused by difficulties in separating the F_2 classes. Between thirteen of these pairs of factors the interrelationship has been fully worked out, whereas a few questions remain unsettled regarding the last two pairs of factors.

Table I gives a list of the factors together with their monofactorial segregation as manifested in the present experiment. Several of these factors will be recognised as being of classical reputation and have accordingly been described several times by different scientists. In those cases I have not thought it necessary to go into details as regards their morphological manifestation, whereas in cases less well known a fuller description has been given.

TABLE I.

List of characters used in the present experiments and their monofactorial distribution in F_2 and backcrosses.

	Factors	F_2 numbers	Backcross
I	1 Round - wrinkled	3006 : 986 = 3.05 : 1	431 : 406 = 1.05 : 1
	2 Tendril - acacia	763 : 239 = 3.19 : 1	444 : 401 = 1.1 : 1
II	3 Yellow - green cot	3778 : 1252 = 3.01 : 1	713 : 699 = 1.02 : 1
	4 Green-yellow pod	2588 : 796 = 3.25 : 1	
III	5 Purple - salmon	2183 : 676 = 3.22 : 1	
	6 Norm stipules - reduced stip	2226 : 743 = 3 : 1	
IV	7 Glaucous^b - emerald^b	2324 : 761 = 3.05 : 1	1065 : 1094 = 0.97 : 1
	8 Wing - keeled wing	1654 : 521 = 3.17 : 1	1087 : 1072 = 1.01 : 1
	9 Colour - white	3859 : 1234 = 3.11 : 1	
	10 Tall - dwarf	3256 : 1089 = 2.98 : 1	
	11 Norm stem - fasc stem	2369 : 701 = 3.37 : 1	
	12 Fertile - sterile	2003 : 682 = 2.93 : 1	
	13 Glaucous^a - emerald^a	792 : 243 = 3.2 : 1	
	14 Dark axil - light axil	1131 : 402 = 2.81 : 1	
	15 Purple pod - green pod	269 : 78 = 3.46 : 1	

1. *Round seed—wrinkled seed.* This character represents one of the most familiar of Mendel's original examples, and his results have since been confirmed by a great many observers. In some varieties the distinction between round and wrinkled seed is perfectly sharp, whereas in others angular shape and much irregular pitting may occur in genetically round seed. As shown by Gregory (1903) and Darbishire (1908) the seeds can be separated by the shape of their starch grains. In the present experiment all the seed used has been tested microscopically.

2. *Tendril—acacia.* In the acacia variety the tendrils of the leaves are represented by small leaflets. The dominance of the normal tendrilled leaf is not quite complete, the heterozygote having more or less strap-shaped tendrils. This pair of factors was found to be strongly linked to round and wrinkled. (For more details concerning this linkage see below.)

3. *Yellow cotyledon—green cotyledon.* This again forms one of Mendel's classical pairs of factors. Yellow is dominant to green and heterozygotes are indistinguishable from homozygous dominants. In addition to this dominant yellow a pale yellow cotyledon colour also exists, the nature of which will be discussed later on.

4. *Green pod—yellow pod.* A yellow-podded plant appeared as previously mentioned (Pellew and Sverdrup, 1923) in a family of plants with reduced stipules. The character can in early stages often be recognised by the yellowish transparent colour of calyx and flower stalk. The very young pod is green, but goes more and more yellow as it grows bigger, and is in the full-grown stage of a bright yellow colour. During the ripening stages also a yellowing of stem and foliage takes place. The character behaves as a simple recessive to green pod and foliage giving a total ratio of 3·25 : 1 (see Table I). The slight shortness of yellow pod is partly due to a lessened viability, partly to the fact that in some cases yellow pod was crossed with "sterile" (see below) in which cases one had to rely on colour of calyx and flower stalk only for recording. The seeds of this variety were wrinkled and of a pale yellowish colour.

Yellow-podded varieties have been known for a long time and came into the experiments of Mendel. The yellow-podded variety used in the present experiments has never been crossed to other yellow-podded varieties but most likely they are all due to the same factor.

5. *Purple—salmon.* The present experiment only deals with two

TABLE II.

Distribution of purple and salmon in F_2 families of the year 1921 *and* 1924–25 *respectively.*

		Purple	Salmon
1921	Actual number	973	266
	Ratio	3.141	0 859
	D	+ 0 141	+ 0 141
	M_k	± 0 049	± 0.049
1924-25	Actual number	1210	410
	Ratio	2 988	1 012
	D	+ 0 012	- 0 012
	M_k	± 0.043	± 0.043
Total	Actual number	2183	676
	Ratio	3 054	0 946
	D	- 0 054	+ 0.054
	M_k	± 0.032	± 0.032

D = deviation from expected ratio.
M_k = standard error.

shades of colours in the flower, purple and salmon, which, in the presence of a ground factor for colour, show a monofactorial difference. Tedin (1920) describes two new flower colours, violet and light purple, and comes to the conclusion that three elements are concerned in building up colours in *Pisum*. As according to his scheme the difference between pure purple and pure salmon remains monofactorial this will, however, not interfere with the result given here.

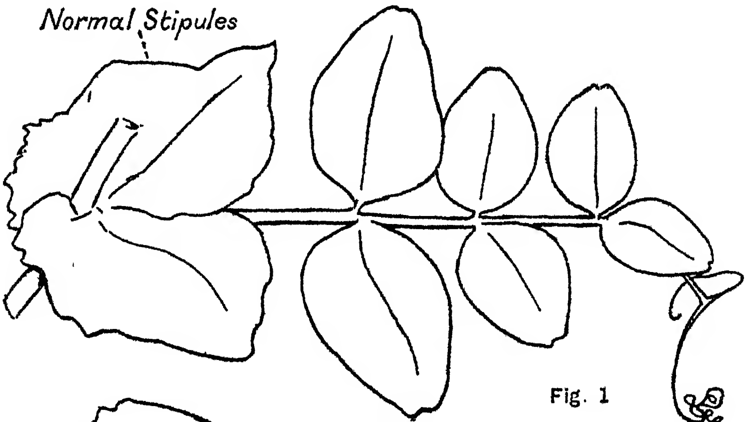

Fig. 1

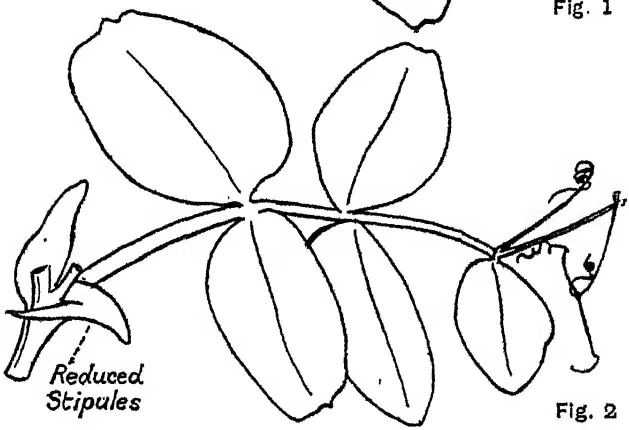

Fig. 2

The total F_2 numbers obtained go slightly in the favour of purple. Table II shows that this shortness of salmon is altogether confined to the year 1921. Even in this year, however, the deviation from expected ratio is hardly big enough to be of any significance. It seems moreover unlikely that if a particular reason exists for the aberrant ratio of 1921 this should not also be present in some of the families of the year 1924 or 1925.

6. *Normal stipules—reduced stipules.* As mentioned in an earlier paper (Pellew and Sverdrup, 1923), a single plant with reduced stipules (Text-figs. 1 and 2) appeared spontaneously in 1915 in a row of the variety Duke of Albany raised from seed obtained from Messrs Sutton (Plates XVIII and XIX). The plant bred true to the new character. Reduced stipules behaves as recessive to normal stipules, the total F_2 number being 2226 normal to 746 reduced. Wellensieck (1925 *a*) remarks upon the fact that Brotherton (1923) found dominance of the smaller form of stipules, whereas Pellew and Sverdrup found dominance of the broader type. Brotherton worked with "rogue" peas, a form which, as shown by Bateson and Pellew (1915 and 1920), always behaves as a dominant, otherwise giving a very peculiar form of segregation. The form with reduced stipules described here has nothing to do with the narrow stipules and leaflets of the "rogue" pea. As already mentioned in our paper, reduced stipules was crossed to Duke of Albany type *and* rogue giving F_1 normal, that is with well-developed stipules, in the one case of the broad normal shape and in the other case of the narrower rogue shape.

7. *Glaucous^b—emerald^b.* Varieties with very little or no wax on foliage and pods are called emeralds. The plants are of a very dark green colour as compared with the greyish colour of the normal plants. Vilmorin (1911) proved that two kinds of emeralds exist, which crossed together give glaucous, both being recessive to glaucous. The emerald of the present pair of factors is the "pois chenille" of Vilmorin, in which the absence of wax is most pronounced in stipules and pods, but not so conspicuous in leaflets. In ripe pods the seeds adhere to each other. The nature and inheritance of this "brochetting" of the peas will not be discussed here as investigations concerning this question are still going on.

8. *Normal wings—keeled wings.* As mentioned earlier (Pellew and Sverdrup, 1923), this form came to us through Messrs Sutton. The flower is very peculiar in that its wings have been transformed into the likeness of the keel. On Plate XVII (Figs. 4 and 7) are shown the normal purple and salmon flowers and (Figs. 5 and 6) their corresponding keeled wing forms. The wings more or less take on the colour of the keel, giving a much paler appearance to the whole flower. Fig. 1 of the same plate gives the structure of the "keeled" wing in more detail, showing in what a strong degree it resembles a normal keel. The segregation in F_2 as well as in backcrosses proved the difference to be monofactorial (see Table I).

9. *Colour—white.* A ground factor for colour exists in the absence of which flowers and leaf axils are colourless, that is, with white flowers and green axils.

10. *Tall—dwarf.* The dwarf varieties used in these experiments had a small number of short internodes and their height did not exceed one to one and a half feet. Dwarfs segregated out perfectly clearly and no difficulties were found in recording the F_2 plants.

11. *Normal stem—fasciated stem.* In fasciated varieties the position of the flowers is terminal, being mostly found at the top of the fasciated stem. The character does not become apparent until the plant has reached a certain height and is also, as found by Lock (1907), to some degree dependent upon environmental influence. In my experience fasciation shows more easily in dwarf than in tall plants. Probably both the above-mentioned reasons account for the shortness of fasciated plants found in F_2, a shortness found also by Kappert (1924) and to a smaller degree by Mendel.

12. *Fertile—sterile.* A very peculiar form (Plate XVIII, fig. 1) appeared in 1914 in a crop of the variety Duke of Albany grown for the purpose of studying rogues in *Pisum*. It was described as a rogue of extremely low grade by Bateson and Pellew (1915), who also give a photograph of the leaf showing the peculiar narrow leaflets. The same form was also found in a commercial crop of Gradus peas. On Plate XVIII, fig. 2, is shown a photograph of a branch of this form and a leaf with its stipules in natural size. Coloured pictures of the flower are given on Plate XVII (Figs. 8 and 9). The stipules are pointed and narrow compared with the normal form. The leaflets are almost strap-shaped and the neuration abnormal, the nerves running much more parallel to the axis of the leaflet than usual; very often the juxtaposition of the leaflets is altered so that they alternate along the stalk instead of being in pairs. The whole texture of the green part of the plant seems coarser and slightly crumpled. The most striking feature of the flower is the standard which is very straight and narrow and drawn out into a long point. The wings are smaller and open up more than in a normal flower, disclosing the whole of the keel. This peculiar form is (with possibly one or two exceptions) completely sterile on its female side. The carpels are deformed and always remain open; as the figure shows, one side overlaps the other. The ovules themselves appear to be well developed as can be seen in the very young pod. The pod generally withers away shortly after the petals have fallen off. In rare cases, however, especially this last summer, some of them were found to de-

velop further and in two cases were found to contain a single-normal-sized pea, both of which had unfortunately been badly eaten by the pea-weevil. Nothing therefore is known as to whether these accidentally developed peas would germinate. The anthers are fully developed and the pollen is normal; the variety therefore can be, and has to a large degree been used as a male. In crosses with normal plants the F_1 has always been found to be normal; the whole complex of difference was found to be due to a single factor, the total F_2 numbers being 2003 normals to 682 steriles or a ratio of 2·93 : 1.

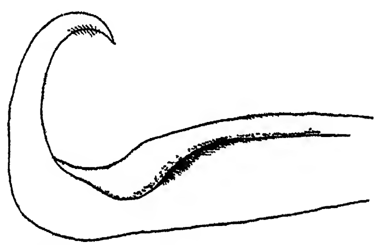

Fig. 3. Sketch from young pod of sterile plant showing abnormal development of carpels.

A very similar form has been described by Nilsson-Leisner (1924). The leaflets of his form, however, are evidently of a still narrower type and the shape of the flower differs in several respects, its standard being very narrow and its wings deeply cut. Like the above-described form, this form was a female sterile with carpels remaining open. The form was used as a male and gave F_1 normal; but it is stated never to have appeared again in F_2 nor in any later generations.

13. *Glaucous^a—emerald^a.* As mentioned above two different kinds of emeralds exist in *Pisum*. Emerald^a (emerald acacia) came to us through Sutton. Crossed to emerald^b it gives glaucous and it is probably the same character as the one described by Vilmorin in his variety "Emereva." It differs from emerald^b in showing no adherence of seed in mature pods. The viability of this form seems to be slightly lowered.

14. *Dark axil—light axil.* No colour in axils, or as it is called here "light axil," was introduced into these experiments through "Solo," a variety received in 1918 from W. Brotherton (presumably the same as the Svalöf variety "Solo"). It was a tall form with purple flowers and yellow round seed in a grey purple-spotted coat. The F_2 numbers in Table I have of course only been taken from plants in which the ground factor for colour was also present. The numbers seem to indicate a slight excess of light axil, but hardly big enough to be more than accidental.

15. *Purple pod—green pod.* Purple pod only went into a few families of these experiments but is included here because there is some indication of linkage to purple and normal stipules. F_2 gave too many purple pods, but the numbers are much too small for a conclusive result on this point.

INTERRELATION OF FACTORS.

In Table III at the end of this paper all the actual data are to be found concerning the interrelationship of the above-described characters. For deciding the question of linkage between two pairs of factors it is always desirable to have F_2's from crosses made up both ways, that is to say from F_1's of the DD′ × RR′ as well as from the DR′ × D′R type. This has been done to as great an extent as was possible without delaying the experiment too much[1]. In working out the expected ratio in each case the specific monofactorial segregation of the two factors in question has been taken into consideration; a deviation between calculated and observed numbers therefore when exceeding three times the probable error can only be due to linkage phenomena. The result obtained from Table III is shown diagrammatically in Text-fig. 2 (p. 224) and described in the following pages.

A. *Linkage groups.*

Among the fifteen characters dealt with here four linked groups have been found, represented by the eight factors of the diagram, each of the groups accordingly containing two pairs of factors. Besides, factor 15—the factor for purple pod—will probably fall into Group III, indications of linkage to purple flower colour and normally developed stipules having been found.

$$\text{Group I} \begin{cases} \text{Round—wrinkled cotyledon.} \\ \text{Tendril—acacia.} \end{cases}$$

The acacia—wrinkled linkage represents the first linkage ever recognised in *Pisum*. Full data were given by Vilmorin and Bateson in 1911 showing that a strong coupling exists between the two factors represented by a gametic ratio of about 63 : 1. Shortly afterwards their result was confirmed by C. Pellew (1913) in an extensive experiment in which repulsion as well as coupling were tested.

The factors were brought into this experiment chiefly for the purpose of trying them with other factors. The F_2 numbers (Table III, 1–2)

[1] The advantage of this method was particularly evident in crosses involving the factors for dwarfness and fasciated stem (see p. 238).

confirmed earlier results. Backcrosses were, however, also undertaken in order to find out whether the male and female showed any perceptible difference in linkage value. Table IV gives the result obtained together with some expected ratios. Unfortunately the numbers of plants are far too small for any definite conclusion; especially in cases of very high linkage like the present one the backcrossing will have to be carried out on a much larger scale. Superficially it looks as if the linkage value found in these backcrosses is considerably lower than the one derived

TABLE IV.

Backcrosses showing strength of linkage on the male and female side within the first linkage-groups.

	Tendril Round	Tendril Wrinkled	Acacia Round	Acacia Wrinkled	
Actual numbers	232	9	1	230	♀ side
Exp on a 46·2 : 1 basis	231	5	5	231	
Exp. on a 63 : 1 basis	232.3	3.7	3.7	232.3	
Actual numbers	195	8	3	159	♂ side
Exp on a 32·1 : 1 basis	177	5.5	5.5	177	
Exp on a 63 : 1 basis	179.6	2.9	2.9	179.6	

No definite indication of an actual difference is present.

from F_2 families. The female side gives a gametic ratio of 46·2 : 1 corresponding to a crossover-percentage of 2·1. On the male side a still lesser value is found, the gametic ratio being 32·1 : 1, which would give about 3 per cent. of crossovers. The calculated numbers, however, show that even a gametic ratio of 63 : 1 gives a fairly good fit. Under these circumstances no stress can be laid upon the difference found between the male and female side. This question will be fully treated under Group IV.

Group II { Yellow cotyledon—green cotyledon.
Green pod—yellow pod.

At the beginning of these experiments it was suggested (Pellew and Sverdrup, 1923) that a triple allelomorphic series existed in *Pisum* composed as follows: (*a*) true dominant yellow cotyledon associated with green pods, (*b*) green cotyledons also associated with green pods and (*c*) pale yellow cotyledons associated with yellow pods, the three standing in a descending order. In 1923, however, a yellow-podded plant came from dominant yellow seed in F_2 from the cross "dwarf, stipless, yellow pod" (pale cot. yellow pod) and Solo (yellow cot. green pod). By crossing

it back to pure green this plant was proved to be a real dominant yellow, the crossed pods giving equality of yellow and green. In the following years more plants of this class appeared, showing that we are here dealing with linkage instead of multiple allelomorphism. The total F_2 numbers obtained are:

	Yellow cot. green pod	Yellow cot. yellow pod	Green cot. green pod	Pale cot. to green yellow pod
	756	21	35	236
Expected on a 17 : 1 basis	758	27·9	27·9	234

The linkage value as calculated from the formula given by Emerson (1916) is 17·3 : 1 or 5·5 per cent.

It remains to say a few words concerning the nature of the pale yellow cotyledon colour which was introduced through the yellow-podded variety. This colour was found to be subject to a great deal of variation, presumably due to the effect of bleaching. Thus three yellow-podded plants from pale yellow seeds were harvested and their seeds examined pod by pod; they were found to contain green and pale yellow seeds, the greens and pales, however, coming in separate pods. All the seed being genetically pale yellow, this character therefore must depend upon certain environmental conditions for its manifestation, these conditions probably being the amount of sun and light to which the pods are exposed. It may be stated here, that the bleaching effect produced in these seeds is different from the one found in a great many green varieties, when a smaller or bigger patch of pale to yellowish green may be found in the seed according to how much of it has been exposed to the sun. In the present case the cotyledon colour is a uniform pale yellow.

The next question which arises is whether this pale yellow cotyledon colour always gives rise to yellow-podded plants or whether we are here dealing with a separate character determined by a factor different from the one determining yellow pod. Pale yellow being introduced through a yellow-podded variety it seemed *a priori* most likely that this colour represented an early manifestation of the factor which later on makes the foliage and the pods of the plants go yellow. The answer to this question as given by the breeding experiments is, however, not quite clear, but as far as it goes is in favour of a correlation such as the one just mentioned. The numbers given below are all from 1924 plants and 1923 seeds. In 1924 it was found impossible to separate greens from pale yellows probably because of wet weather during the ripening season. The result of the breeding is as follows:

1. *Green and pale yellow* give F_1 all green and in F_2 segregation of green and yellow in a 3 : 1 ratio, the numbers being:

	Green cot.	Yellow cot.
Actual numbers	344	107
Expected numbers	338·3	112·7

The green variety used in the cross was "emerald brochette" which has a very dark green cotyledon colour not given to bleaching. Green and yellow pods were distributed among the F_2 seeds as follows:

	I Green cot. green pod	II Green cot. yellow pod	III Pale cot. green pod	IV Pale cot. yellow pod
Observed	332	12	20	87
Expected on a 13 : 1 basis	326·2	12·05	12·05	100·7

The existence of Class III (pale cot. green pod) goes in favour of a specific factor for pale yellow cotyledon colour independent of the factor for yellow pod and foliage. The F_2 numbers suggest a linkage between pale yellow seeds and yellow pods. Calculated from Emerson's formula (1916) the gametic ratio was found to be 13 : 1, from which the expected numbers are deduced.

This is in agreement with the results obtained by O. E. White (1916). He found green cotyledon to be dominant to the yellow cotyledon of the yellow-podded variety "Goldkönig," and in 1917 he gives the following numbers showing the interrelation between pale yellow cotyledon and yellow foliage:

	I Green cot. green foliage	II Green cot. yellow foliage	III Yellow cot. green foliage	IV Yellow cot. yellow foliage
	134	6	16	40
Expected on a 13 : 1 basis	140·2	6·8	6·8	32·2

These numbers, like the ones from the present experiment, point to an existing linkage; they are, as already mentioned by White, too small for settling the linkage value; the agreement to the value found above is, however, fairly good.

So far everything seemed quite clear. I should, however, like to point out the possibility of the pale yellow cotyledon of Class III being due to bleaching, because, although the "emerald brochette" is a non-bleaching variety, yet it must be remembered that the yellow-podded variety came from "Duke of Albany," the cotyledon of which is apt to bleach; the tendency for bleaching, therefore, may have been introduced into the cross through yellow pod.

2. *Dominant yellow and pale yellow.* F_2 numbers from this cross give no support to the result reached above. Assuming green and pale cotyledon to be due to different factors, one would expect in F_2 from this cross dominant yellows, greens and pales in proportion 12 : 3 : 1 or 9 : 3 : 4 according to whether the cotyledon of a seed homozygous for pale yellow and carrying dominant yellow would be phenotypically dominant yellow or pale. The following F_2 numbers do not agree with any of these stipulations:

I Dom. yellow	II Green	III Pale yellow
263	14	66

The deficiency of green is too big to fit either of those two schemes. The distribution of the pod colour is given below; again a few pale yellow seed gave green pod.

I Dom. yellow green pod	II Dom. yellow yellow pod	III Green green pod	IV Green yellow pod	V Pale green pod	VI Pale yellow pod
261	2	9	5	6	60

Class V may again be accounted for by assuming bleaching of genetically green cotyledons or in this case perhaps also partly through mistaking dominant yellow cotyledon for pale yellow.

At present there seems to be no scheme wherewith it is possible to bridge over the strong disagreement between the two crosses given above. But I feel most inclined to regard the recessive pale yellow cotyledons simply as an early manifestation of the factor for yellow pod.

Group III { Purple flowers—salmon flowers.
Normal stipules—reduced stipules.

As mentioned in a previous paper (Pellew and Sverdrup, 1923), this linkage was first found in 1921 in a cross between a white variety with

TABLE V.

F_2 numbers from the third linkage group showing result of DR × DR as well as DD × RR crosses.

	Purple flowers Normal stip.	Purple flowers Reduced stip.	Salmon flowers Normal stip.	Salmon flowers Reduced stip.	
F_2 from DR×DR	249	105	106	4	1922
Exp. on 1 : 2.5 basis	241.5	106.5	106.5	9.5	
Exp. on 1 : 3.6 basis	237.5	110.5	110.5	5.5	
F_2 from DD×RR	150	26	18	34	1925
Exp. on 1 : 3.6 basis	148.9	22.09	22.09	34.9	

reduced stipules and a salmon variety having normal, the factors consequently going in DR × DR. In Table V are found the earlier published numbers together with some more F_2 numbers from a cross of the DR × DR type. The value of this linkage was in 1922 found to be represented by a gametic ratio of 1 : 2·5. The second lot from the DD × RR cross give a somewhat higher value, the gametic ratio calculated to be about 3·6 : 1. No importance can, however, be paid to this apparent discrepancy as the numbers are too small. The gametic ratio is probably about 3 : 1. It is hoped that the actual strength of this linkage will be finally settled next summer as a considerable number of seeds from backcrossing both ways have been obtained.

Besides these two factors the factor for purple pod has been found to belong to this group. The numbers given in Table VI plainly show purple pod to be linked to reduced stipules and purple; but the actual

TABLE VI.

F_2 numbers showing linkage between normal stipules and purple pod.

The cross was made DD × RR.

	Normal stip Pur. pod	Normal stip. Gr. pod	Reduced stip. Pur. pod	Reduced stip Gr. pod
Actual numbers	40	15	1	8
Exp. on a 15 : 1 basis	38.9	1.6	1.6	11.9

TABLE VII.

F_2 numbers showing linkage between purple flower colour and purple pod.

The cross was made DD × RR.

	Pur. pod Purple	Pur. pod Salmon	Green pod Purple	Green pod Salmon
Actual numbers	82	17	14	13
Exp. on a 2.5 : 1 basis	79.07	15.4	15.4	16.07

strength of these linkages cannot be definitely settled till bigger numbers are produced. So far a linkage of gametic value 15 : 1 is suggested between reduced stipules and purple pod, whereas apparently the linkage between purple pod and purple is of a much lower order. An experiment involving all three factors is in progress and results from F_2 families as well as from backcrosses will be available next year; it is hoped that these crossings will also give some information concerning double crossovers in *Pisum*.

Group IV $\begin{cases} \text{Glaucous}^{b}\text{—emerald}^{b}. \\ \text{Normal wings—keeled wings.} \end{cases}$

Together with the one just described this linkage was first published in 1923 (Pellew and Sverdrup). The F_2 numbers were derived from the cross glaucous foliage and keeled winged flowers × emerald foliage and normal flowers, the cross therefore being of the DR × DR type. To these numbers can now be added the result from a cross of the other type, glaucous, normal wings × emerald keeled wings. Both results are given in Table VIII.

TABLE VIII.

F_2 numbers from the fourth linkage group showing result of DR × DR as well as DD × RR crosses.

	Glaucous^b Normal wings	Glaucous^b Keeled wings	Emerald^b Normal wings	Emerald^b Keeled wings
F_2 from DR × DR	374.	174	164	5
Exp on 1:3.2 basis	368.6	169.1	169.1	10.2
Exp. on 1:6.8 basis	361.1	176.5	176.5	2.9
♀ 1:11 3, ♂ 1:6.8	359 4	176.9	176.9	1.84
F_2 from DD × RR	219	21	17	61
Exp. on 1:6.8 basis	219.2	19.3	19.3	60.2
♀ 1:11.3, ♂ 1:6.8	223.5	15.7	15.7	63.8

Again a rather striking difference in linkage value is found between the two types. The gametic ratio was at first calculated to be about 1 : 4. Using Emerson's formula, however, the gametic ratio from the DR × DR cross will be 1 : 3·2, whereas the ratio as calculated from the DD × RR is 6·8 : 1. The numbers though bigger than in the previous case are, however, still too small for any conclusion as to the significance of this difference and it must also be remembered that the two lots of plants were grown in different years and therefore not under strictly the same external conditions. It might, however, be of interest in this connection to mention that Nabours (1925) in his latest paper on *Apotettix* found a similar difference in linkage value between "repulsion" and "coupling" (see Table VII of his paper). His data which are derived from backcrosses are very extensive and the difference found sometimes considerable, as for instance between his factors M and O. Nabours suggested that this high degree of variability may be due to the great extremes of external conditions to which his cultures had been exposed and perhaps also to variation-factors brought in through

different geographical strains. Whether this explanation covers the ground further experiments must decide. Moreover, Demerec (1926) in a recent paper remarks upon the same discrepancy between "coupling" and "repulsion," which he finds in a linkage experiment in Maize. The same phenomena has further lately been recorded by Imai (1926) from experiments with the Japanese Morning Glory.

Owing to its smaller strength this linkage seemed to offer more favourable conditions for testing a possible difference in linkage value between the two sexes. Backcrossing was accordingly undertaken on as big a scale as possible. Anybody working with peas will know that it is not a material which lends itself easily to the process of backcrossing. At the very best only an average of five to six peas per pod can be expected and very often the result of one's labour is spoilt by bad weather or other external influence during the ripening season. The summer of 1924, however, proved to be a lucky one for this undertaking. The plants were large and healthy and seed setting exceptionally good. But even so I should not have been able to carry it through without the valuable help given me by Miss de Winton. More than 2000 seeds were obtained and practically all of these germinated the next summer. The heterozygotes used were all from the same F_1 of the DD × RR type, the same plants from which the F_2 families given in Table VIII were raised. The result of this backcrossing is given in Table IX. The linkage as calcu-

TABLE IX.

Backcrosses showing difference in strength of linkage on male and female side within the fourth linkage group.

	Glaucous^b Normal wings	Glaucous^b Keeled wings	Emerald^b Normal wings	Emerald^b Keeled wings	
Actual numbers	447	35	44	446	♀ side
Exp. on a 11.3 : 1 basis	446.5	39.5	39.5	446.5	
Exp. on a 6.8 : 1 basis	414.7	71.3	71.3	414.7	
Actual numbers	516	69	82	516	♂ side
Exp. on a 6.8 : 1 basis	516	75.5	75.5	516	
Exp. on a 11.3 : 1 basis	543.4	48.1	48.1	543.4	

lated from these numbers proved to be stronger on the female side, the gametic ratio being 11·3 : 1 on the female as compared to 6·8 : 1 on the male side, giving a crossover percentage of 8·12 and 12·8 respectively. With as big numbers as these and with all the plants grown under exactly the same conditions it seems to me to be a safe conclusion that we are here dealing with a real difference between the two sexes. In

Table VIII expected numbers have been worked out in which this difference has been taken into due consideration. As the linkage in the "repulsion" case has already been found to be a good deal lower, it is not astonishing that the agreement here is not very good. Even in the case of "coupling" the linkage appears to be slightly lower than the one established by the backcrosses. But this difference is not big enough to be of any significance. Difference in strength of linkage between the two sexes in plants is a well-known phenomenon in *Primula sinensis* (Gregory, Miss de Winton and Bateson, 1923) and here, surprisingly enough, it is found to vary inside the same linkage group, so that between two certain factors the linkage is stronger on the male side, while between two other factors it is stronger on the female side.

B. *Independent inheritance.*

With the four linkage groups just described and with the likelihood of factor 15 belonging to Group III, our number of possible independent

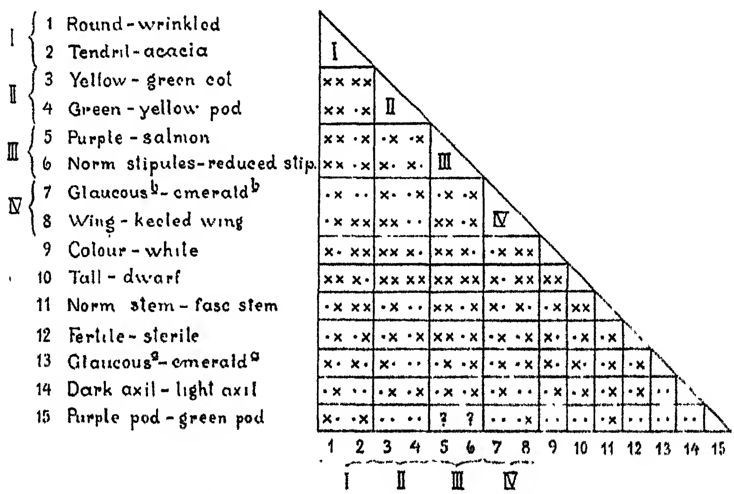

Fig. 4. Diagram illustrating the result from the various crosses made between fifteen pairs of factors. The actual data are found in Table III, at the end of the paper. × × signifies that the cross was made both ways (DD × RR and DR × DR) and no linkage found. × signifies that one cross only was tried, a left-hand cross meaning DD × RR and a right-hand one DR × DR.

factors or factor groups is now reduced to ten. The independent inheritance so far found between these is demonstrated in Text-fig. 4. This diagram shows the number and nature of the various crosses and the results obtained. Altogether 115 different combinations have been tried, 107 of which showed no sign of linkage. In the diagram no

linkage is indicated by a cross. The position of these marks shows in what order the factors went into the cross; a mark to the left stands for a DD × RR cross, a mark to the right for a DR′ × D′R cross and two marks accordingly show that both ways have been tried and no linkage found.

The six big squares in the upper corner of the diagram demonstrate the independence of the four linkage groups between each other. In four cases all the four possible combinations were tried; in two cases only three of these four possible crosses were tested; but even so the possibility of linkage seems to be excluded. Table III (at the end of the paper) gives the figures which form the basis for this evidence; in every case these numbers agree with the numbers that would be expected in the case of free assortment.

The remaining six factors (9–14) have in most cases been tested with both factors inside each linkage group. In doing this one outstanding difficulty when testing linkage from F_2 families has been diminished; as is well-known, very big numbers are here required to distinguish between free segregation and linkage of low value; if, however, a factor shows no linkage to two factors situated in one chromosome, the chance is very small that this factor can belong to this same chromosome, especially if the linkage in question is not a very strong one as is, for instance, the case in Groups II, III and IV of this experiment. In this way factors 9, 10 and 12 were found to be independent of all four groups. Factors 11 and 13 were tested with both factors of three of the groups and factor 14 with both factors inside two groups.

A special test was made to establish the interrelationship between the two kinds of emerald. Emerald^a and emerald^b give in F_1, as already mentioned, plants with glaucous foliage. F_2 from this cross gave glaucous and emerald, but it was found impossible to distinguish between the different emeralds. It is true that some of the plants were found to have adherent seeds as in emerald^b, while other plants had pods with free seed; this however could not be regarded as a safe distinction as it had already been found that white-flowering emerald^b plants are capable of having free seeds; also the exact relationship between emerald^b and brochetting is not yet known. F_2 gave 70 glaucous to 49 emeralds, a result near enough to the expected 9 : 7 ratio of 67 glaucous to 52 emeralds. The numbers are, however, too small for any definite conclusion; but, instead of repeating the cross in order to get more numbers, the factorial constitution of the emeralds appearing in F_2 was tested by crossing these back to both grandparental types. As would be ex-

pected, the emeralds appearing in F_2 proved to be weak plants and several of them died before ripening their seed. Only in ten cases therefore was the scheme carried through successfully. Free segregation would give emeralds of different constitution in the following ratios: 2 hom. em.[b] het. em.[a] : 2 het. em.[b] hom. em.[a] : 1 hom. em.[b] hom. gl.[a] : 1 hom. gl.[b] hom. em.[a] : 1 hom. em.[b] hom. em.[a]. The distribution of the tested plants was: 3 hom. em.[b] het. em.[a] : 2 het. em.[b] hom. em.[a] : 2 hom. em.[b] hom. gl.[a] : 1 hom. gl.[b] hom. em.[a] : 2 hom. em.[b] hom. em.[a]. The backcrossing proved the double recessive to be viable; moreover, the fact of two plants of this kind being found among ten is strongly in favour of no linkage; the factors went in DR′ × D′R and linkage would in this case tend to diminish the numbers of double recessives. Emerald[a] was also tried with the second factor of Group IV, the factor for keeled wing, and no linkage was found.

Finally all but one of all the possible combinations between the six factors outside the linkage groups have been tried and no linkages have been found. The interrelationship between light axil and emerald[a] is as yet not settled. It is perhaps unfortunate that in the case of 9–11, 9–12, 9–13, 10–12, 10–13 and 11–12 only one way of crossing has been tried; but the F_2 numbers are in all these cases in very good agreement with independent inheritance. In one case, 10–12, the two outer terms are slightly too big, but as the factors went into the cross DR′ × D′R this discrepancy from expected numbers can scarcely be due to linkage. The deviation is not big enough to be outside the possibility of random sampling.

Some peculiarity was found in F_2's from crosses between factors 10 and 11. The figures given in Table III show that whether dwarf went in with fasciated or with normal stem the classes containing the top dominants and the double recessives both come out too big. From a DD × RR cross alone this might have led to the conclusion that possibly a linkage of low value was present. But the result from the DR′ × D′R cross makes this assumption untenable; in case of linkage the outer terms should here have come smaller than expected. Kappert (1924) in a DR′ × D′R cross found the same discrepancy, whereas White (1917) gives figures which are in agreement with ordinary free segregation. My experience is, as also found by Lock (1907), that fasciation in tall plants may vary to the extent of giving almost normal plants; in dwarf plants on the other hand fasciation seems to be more strongly manifested and possibly heterozygous plants may be taken for homozygous. No experimental proof is however so far available.

C. *Conclusions.*

The generally accepted and well-founded theory of chromosomal inheritance claims an agreement between the numbers of independent factors and the number of chromosome pairs within any species. This agreement has been adequately proved in different species of *Drosophila*; the more than 300 known genes of *Drosophila melanogaster* thus fall into four groups corresponding to the four pairs of chromosomes. But a similar relation has so far not been established for a certainty within any other genetical material. In *Pisum* one might expect to find a favourable object for a verification of this theory; it is a well-known classical object of genetical research and a comparatively great many factors are known showing simple mendelian segregation; the haploid chromosomal number is seven. In spite of this, however, the attempts made to bring the number of factors and the number of chromosomes into agreement have failed. Kappert (1924) worked out the interrelationship of nine well-known characters; among these he found two to be linked leaving eight to all appearance independent pairs of factors. In the present experiment fifteen factors were involved; fourteen of these were found to fall into four linkage groups, plus five factors which showed no linkage either to the factors of the four groups or among themselves; altogether therefore the number of independent factors and factor groups appeared to be nine, while seven is the number expected from the chromosomal equipment. Moreover, this number will possibly be raised to ten as one of the factors (No. 14 of Text-fig. 4) was found to segregate independently from the four groups and from four of the single factors, leaving only one combination (13–14) untried. The advantage of trying a factor with two or more factors inside a linkage group has already been pointed out; another precaution which has been followed as far as possible is to make up the F_1 families both ways. But even so, when two factors only are concerned, it can always be argued that from an F_2 family of moderate size it is difficult if not impossible to distinguish between free segregation and a linkage of low value. Kappert (1924) points out that in a family of about a thousand plants a linkage percentage beyond 45 cannot be spotted. The result given here therefore cannot be regarded as conclusive, although it is remarkable how very small deviations from expected numbers one finds, even in small families. One can only state that so far the number of factors and the number of chromosomes in *Pisum* fail to show agreement. To my mind this need not necessarily affect the theory of chromosomal

inheritance but does perhaps indicate a looser structure of the chromosomes within certain species.

In this connection may be mentioned a peculiarity found in the structure of the chromosomes of *Pisum*. On examining somatic divisions from root tips one pair of the chromosomes were found to be segmented, having what Nawaschin has termed trabant chromosomes. This is demonstrated in the metaphase shown in Text-fig. 5 where the chromosomes in question can be seen to consist of a small round piece attached by means of a thin thread to the otherwise rod-shaped chromosome. Nawaschin (1912), from his studies of *Galtonia candicans,* is inclined to regard these

Fig. 5. Equatorial plate from somatic division in root tip.

trabants as independent chromosomes comparable to the sex chromosomes of insects, whereas Newton (1924), working on the same material, comes to the conclusion that they represent nothing but a further development of the simple segmentation met with in other chromosomes of the same species. Anyhow, for the present moment, it is not possible to say whether a structure like this in *Pisum* indicates a more flexible composition of the chromosomes; but in the light of the above genetical results one feels inclined to think of it as a possibility.

Abnormal flower on plant heterozygous in keeled wing.

In a family homozygous in fasciation but heterozygous in keeled wing a plant $\frac{119^1}{24}$ appeared having one flower which at first sight looked like keeled wing. On closer inspection, however, the case was found to be more complicated. The abnormal flower is pictured in Figs. 1 and 2 on Plate XVII. Fig. 3 of the same plate gives a normal flower-stalk with its flower, deprived of petals and calyx, in its right position. As seen in Fig. 2 the position of the abnormal flower was upright instead of being at right angles to the pedicel. All the changes appear to be directed centralwards. The standard was divided into two parts, the

colour and structure of which were very much like normal wings. The wings (w) were changed exactly like "keeled wing" but were in addition completely devoid of anthocyanin. The keel (k) was normal. Twelve stamens more or less regularly arranged. Six sepals asymmetrically placed, one ventral, one dorsal with bifid points, and two, partly divided from each other, on each side. Pedicel green with no purple red on its dorsal surface as in normal flowers (see Fig. 3); only articulation red. At basis of pedicel a small stipule-like simple leaf. Pedicel thicker than normal and peduncle thick and flat. As only one flower of the above description appeared, no genetical test could be made and nothing settled as to whether this abnormal development was in any way connected with keeled wing; the rest of the plant gave keeled wing in the ordinary 1 : 3 ratio. A similar abnormality has never been observed in any other family, but it may be mentioned that in fasciated plants flowers with abnormally developed petals are not infrequent; particularly one often finds the standard changing into a more wing-like structure.

SUMMARY.

1. The present investigation deals with the interrelationship of fifteen pairs of easily distinguishable characters in *Pisum*, all of which show a monofactorial segregation. Full descriptions are given only of the less well-known characters, such as have appeared in later years. Among them the most interesting one is a mutation called "sterile"; this form shows peculiar and definite changes in every organ of the plant; no seed is obtained owing to an abnormality in the development of the carpels.

2. Four linkage groups have been found among these fifteen pairs of factors, one containing three, the rest of them two factors respectively. One is the wrinkled-acacia case, well-known from early experiments in *Pisum*. The remaining three were found during the present investigation. Yellow cotyledon proved to be linked to green pod, instead of forming a series of multiple allelomorphs as suggested earlier.

3. Five of the remaining six factors were tested with the factors of the four groups as well as among themselves, and no linkage could be detected. As regards the sixth factor it has so far been found to be independent of the groups and of four of the single factors; one combination remains, however, to be tested.

4. The fifteen characters, therefore, appear to fall into four linkages plus five (possibly six) independent factors, giving in all nine independent groups, whereas from the chromosomal number seven only

would be expected. No satisfactory explanation can so far be given as to the cause of this disagreement.

5. In somatic divisions one pair of the chromosomes was found to be segmented, having what Nawaschin has termed trabant chromosomes.

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[1] Known from references only.

sterile

DESCRIPTION OF PLATES XVII AND XVIII.

Plate XVII.

Figs. 1 and 2. Abnormal flower on plant heterozygous in keeled wing. *s* = standard. *w* = wing. *k* = keel.

Fig. 3. Normal flower, deprived of petals and calyx, showing position of flower and colour of pedicel.

Fig. 4. Purple flower with normal wings.

Fig. 5. Purple flower with keeled wings.

Fig. 6. Salmon flower with normal wings.

Fig. 7. Salmon flower with keeled wings.

Figs. 8 and 9. Purple and salmon flowers from "sterile" plant.

Plate XVIII.

Fig. 1. Branch of dwarf sterile plant.

Fig. 2. Leaf, stipules and flowers from same plant.

TABLE III.

F_2 numbers obtained from various crosses made between 15 *pairs of factors.*

The first row of each cross shows the monofactorial as well as the bifactorial distribution found in each case. The second row gives the monofactorial ratio as found in each case and the expected numbers in case of independent segregation. AB indicates that the two dominants went into the cross together, Ab that one dominant and one recessive came from each side. M = standard error, calculated from the formula $M=\sqrt{\frac{p\,(n-p)}{n}}$. For the factors denoted by the numerals 1–15 see Table I, p. 222.

Factor combination		Original cross	Monofactorial distribution A : a	B : b	Bifactorial distribution AB : Ab : aB : ab	Total	(AB + ab) : (Ab + aB)	Diff.	M
1–2	Round—tendril	AB	326 : 118	325 : 119	322 : 4 : 3 : 115	444	437 : 7	*166·8*	10·3
			2·94 : 1·06	2·93 : 1·07	238·6 : 87·4 : 86·4 : 31·6		270·2 : 173·8		
		AB*	431 : 406	444 : 393	427 : 4 : 17 : 389	837	816 : 21	*396·8*	14·5
			1·03 : 0·97	1·06 : 0·94	228·6 : 202·4 : 215·4 : 190·6		419·2 : 417·8		
1–3	Round—yellow	AB	1322 : 449	1342 : 429	987 : 335 : 355 : 94	1771	1081 : 690	29·6	20·4
			2·99 : 1·01	3·03 : 0·97	1001·8 : 320·2 : 340·2 : 108·8		1110·6 : 660·4		
		Ab	699 : 232	719 : 212	540 : 159 : 179 : 53	931	593 : 338	0·4	14·7
			3 : 1	3·09 : 0·91	539·8 : 159·2 : 179·2 : 52·8		592·6 : 338·4		
1–4	Round—green pod	AB	541 : 179	546 : 174	410 : 131 : 136 : 43	720	453 : 267	0·6	11·3
			3·01 : 0·99	3·03 : 0·97	410·3 : 130·7 : 135·7 : 43·3		453·6 : 266·4		
		Ab	40 : 15	41 : 14	28 : 12 : 13 : 2	55	30 : 25	3·6	3·6
			2·91 : 1·09	2·98 : 1·02	29·8 : 10·2 : 11·2 : 3·8		33·6 : 21·4		
1–5	Round—purple	AB	226 : 78	226 : 78	165 : 61 : 61 : 17	304	188 : 116	6·0	8·5
			2·97 : 1·03	2·97 : 1·03	168 : 58 : 58 : 20		182 : 122		
		Ab	798 : 255	817 : 236	622 : 176 : 195 : 60	1053	682 : 371	5·7	15·6
			3·03 : 0·97	3·10 : 0·90	619·2 : 178·8 : 197·9 : 57·1		676·3 : 376·7		
1–6	Round—stipules	AB	978 : 296	981 : 293	766 : 212 : 215 : 81	1274	847 : 427	25·8	17·1
			3·07 : 0·93	3·08 : 0·92	753·1 : 224·9 : 227·9 : 68·1		821·2 : 452·8		
		Ab	40 : 15	42 : 13	29 : 11 : 13 : 2	55	31 : 24	3·1	3·6
			2·91 : 1·09	3·05 : 0·95	30·5 : 9·4 : 11·4 : 3·5		34·1 : 20·9		
1–7	Round—glaucous[b]	AB	1041 : 339	1046 : 334	805 : 236 : 241 : 98	1380	903 : 477	32	17·9
			3·02 : 0·98	3·1 : 1	789 : 252 : 256 : 82		871 : 509		

1–8	Round— wing	Ab	888 : 267 3·08 : 0·92	845 : 310 2·93 : 1·07	650 : 238 : 195 : 72 649·7 : 238·3 : 195·3 : 71·7	1155	722 : 433 721·4 : 433·6	0·68	16·5
1–9	Round— colour	AB	3149 : 1017 3·02 : 0·98	3158 : 1008 3·03 : 0·97	2391 : 758 : 767 : 250 2387·1 : 761·9 : 761·9 : 246·1	4166	2641 : 1525 2633·2 : 1532·8	7·8	31·1
1–10	Round— tall	AB	705 : 265 2·91 : 1·09	749 : 221 3·09 : 0·91	549 : 156 : 200 : 65 544·4 : 160·6 : 204·6 : 60·4	970	614 : 356 604·8 : 365·2	9·2	15·1
		Ab	873 : 283 3·02 : 0·98	853 : 303 2·95 : 1·05	639 : 234 : 214 : 69 644·2 : 228·8 : 208·8 : 74·2	1156	708 : 448 718·4 : 437·6	10·4	16·1
1–11	Round— norm. stem	Ab	1520 : 515 2·99 : 1·01	1583 : 452 3·11 : 0·89	1181 : 339 : 402 : 113 1182·4 : 337·6 : 400·6 : 114·4	2035	1294 : 741 1296·8 : 738·2	2·8	21·7
1–12	Round— fertile	Ab	1622 : 523 3·02 : 0·98	1629 : 516 3·04 : 0·96	1233 : 389 : 396 : 127 1231·8 : 390·2 : 397·2 : 125·8	2145	1360 : 785 1357·6 : 787·4	2·4	22·3
1–13	Round— glaucous[a]	AB	622 : 227 2·93 : 1·07	638 : 211 3·09 : 0·91	458 : 164 : 180 : 47 467·4 : 154·6 : 170·6 : 56·4	849	505 : 344 523·8 : 325·2	18·8	14·2
1–14	Round— dark axil	Ab	427 : 139 3·02 : 0·98	400 : 166 2·83 : 1·17	298 : 129 : 102 : 37 301·7 : 125·2 : 98·2 : 40·7	566	335 : 231 342·4 : 223·4	7·6	11·6
1–15	Round— purple pod	AB	53 : 15 3·12 : 0·88	41 : 27 2·41 : 1·59	30 : 23 : 11 : 4 31·9 : 21·1 : 9·1 : 5·9	68	34 : 34 37·8 : 30·2	3·8	4·1
2–3	Tendril— yellow	AB	458 : 174 2·90 : 1·10	469 : 163 2·97 : 1·03	337 : 121 : 132 : 42 339·8 : 118·2 : 129·2 : 44·8	632	379 : 253 384·6 : 247·4	5·6	12·3
		Ab	57 : 18 3·04 : 0·96	55 : 20 2·93 : 1·07	43 : 14 : 12 : 6 41·8 : 15·2 : 13·2 : 4·8	75	49 : 26 46·6 : 28·4	2·4	4·2
2–4	Tendril— green pod	Ab	107 : 21 3·34 : 0·66	104 : 24 3·25 : 0·75	88 : 19 : 16 : 5 86·9 : 20·1 : 17·1 : 3·9	128	93 : 35 90·8 : 37·2	2·2	5·1
2–5	Tendril— purple	Ab	281 : 102 2·93 : 1·07	307 : 76 3·21 : 0·79	221 : 60 : 86 : 16 225·4 : 55·7 : 81·8 : 19·9	383	247 : 146 245·3 : 137·5	8·5	9·4
2–6	Tendril— stipules	Ab	221 : 61 3·13 : 0·87	227 : 55 3·22 : 0·78	182 : 39 : 45 : 16 177·9 : 43·1 : 49·1 : 11·9	282	198 : 84 189·8 : 92·2	8·2	7·9
2–8	Tendril— wing	AB	136 : 39 3·11 : 0·89	125 : 50 2·86 : 1·14	98 : 38 : 27 : 12 97·1 : 38·9 : 27·9 : 11·1	175	110 : 65 108·2 : 66·8	1·8	6·4
		Ab	97 : 35 2·94 : 1·06	104 : 28 3·15 : 0·85	80 : 17 : 24 : 11 76·4 : 20·6 : 27·5 : 7·4	132	91 : 41 83·8 : 48·1	7·1	5·5

TABLE III (*continued*).

Factor combination		Original cross	Monofactorial distribution A : a	Monofactorial distribution B : b	Bifactorial distribution AB : Ab : aB : ab	Total	(AB + ab) : (Ab + aB)	Diff.	*M*
2–9	Tendril— colour	AB	271 : 99 2·93 : 1·07	281 : 89 3·04 : 0·96	206 : 65 : 75 : 24 205·8 : 65·2 : 75·2 : 23·8	370	230 : 140 229·6 : 140·4	0·4	9·3
		Ab	223 : 61 3·14 : 0·86	227 : 57 3·20 : 0·80	178 : 45 : 49 : 12 178·2 : 44·7 : 48·7 : 12·2	284	190 : 94 190·4 : 93·4	0·6	7·9
2–10	Tendril— tall	AB	615 : 204 3·00 : 1·00	625 : 194 3·05 : 0·95	475 : 140 : 150 : 54 469·3 : 145·7 : 155·7 : 48·3	819	529 : 290 517·6 : 301·4	11·4	13·8
2–11	Tendril— norm. stem	AB	193 : 57 3·09 : 0·91	196 : 54 3·14 : 0·86	148 : 45 : 48 : 9 151·3 : 41·7 : 44·7 : 12·3	250	157 : 93 163·6 : 86·4	6·6	7·5
		Ab	245 : 92 2·91 : 1·09	244 : 93 2·90 : 1·10	173 : 72 : 71 : 21 177·4 : 67·6 : 66·6 : 25·4	337	194 : 143 202·8 : 134·2	8·8	9·0
2–12	Tendril— fertile	Ab	268 : 93 2·97 : 1·03	286 : 75 3·14 : 0·86	212 : 56 : 74 : 19 212·3 : 55·7 : 73·7 : 19·3	361	231 : 130 231·6 : 129·4	0·6	9·1
2–13	Tendril— glaucous[a]	AB	591 : 202 2·98 : 1·02	623 : 170 3·14 : 0·86	464 : 127 : 159 : 43 464·3 : 126·7 : 158·7 : 43·3	793	507 : 286 507·6 : 285·4	0·6	13·5
2–14	Tendril— purple pod	Ab	93 : 33 2·95 : 1·05	96 : 30 3·05 : 0·95	70 : 23 : 26 : 7 70·8 : 22·1 : 25·1 : 7·8	126	77 : 49 78·6 : 47·2	1·8	3·7
3–4	Yellow— green pod	AB	776 : 272 2·96 : 1·04	792 : 256 3·02: 0·98	756 : 20 : 36 : 236 586·5: 189·5 : 205·5 : 66·5	1048	992 : 56 653 : 395	*339*	15·7
3–5	Yellow— purple	Ab	1039 : 316 3·07 : 0·93	1054 : 301 3·08 : 0·93	805 : 234 : 249 : 67 808·2 : 230·8 : 245·8 : 70·2	1355	872 : 483 878 ·4: 476·3	6·4	17·6
3–6	Yellow— stipules	AB	666 : 202 3·07 : 0·93	648 : 220 2·99 : 1·01	495 : 171 : 153 : 49 497·3 : 168·8 : 150·8 : 51·2	868	544 : 324 548 : ·4319·6	4·4	14·2
3–7	Yellow— glaucous[b]	AB	1456 : 515 2·96 : 1·04	1504 : 467 3·05 : 0·95	1119 : 337 : 385 : 130 1111 : 345 : 393 : 122	1971	1249 : 722 1233 : 738	16	21·5
		AB*	713 : 699 1·01 : 0·99	705 : 707 1 : 1	367 : 346 : 338 : 361 356 : 357 : 349 : 350	1412	728 : 684 706 : 706	22	18·9
3–8	Yellow— wing	AB	205 : 75 2·93 : 1·07	211 : 69 3·01 : 0·99	158 : 47 : 53 : 22 154·5: 50·5 : 56·5 : 18·5	280	180 : 100 173 : 107	7·0	8·1
		Ab	1039 : 347 3·0 : 1·0	1049 : 337 3·03 : 0·97	779 : 260 : 270 : 70 786·4 : 252·6 : 262·6 : 84·4	1386	856 : 530 870·8: 515·2	14·8	17·9

		AB*	713 : 699 1·01 : 0·99	711 : 701 1·01 : 0·99	360 : 353 : 351 : 348 359 : 354 : 352 : 347	1412	708 : 704 706 : 706	2·0	18·9
3–9	Yellow—colour	AB	1093 : 327 3·08 : 0·92	1015 : 405 2·86 : 1·14	775 : 318 : 240 : 87 781·3 : 311·7 : 233·7 : 93·3	1420	862 : 558 874·6 : 545·4	12·6	18·3
		Ab	760 : 229 3·07 : 0·93	765 : 224 3·09 : 0·91	593 : 167 : 172 : 57 587·8 : 172·5 : 176·9 : 51·8	989	650 : 339 639·6 : 349·4	10·4	15·0
3–10	Yellow—tall	AB	2405 : 771 3·03 : 0·97	2386 : 790 3·01 : 0·99	1790 : 615 : 596 : 175 1806·8 : 598·2 : 579·2 : 191·8	3176	1965 : 1211 1998·6 : 1177·4	33·4	27·2
		Ab	202 : 56 3·19 : 0·81	189 : 69 2·99 : 1·01	144 : 58 : 45 : 11 148 : 54 : 41 : 15	253	155 : 103 163 : 95	8·0	7·8
3–11	Yellow—norm. stem	Ab	1140 : 376 3·01 : 0·99	1183 : 333 3·12 : 0·88	892 : 248 : 291 : 85 889·6 : 250·4 : 293·4 : 82·6	1516	977 : 539 972·2 : 543·8	4·8	18·7
3–12	Yellow—fertile	Ab	1085 : 323 3·08 : 0·92	1049 : 359 2·98 : 1·02	805 : 280 : 244 : 79 808·4 : 276·6 : 240·6 : 82·4	1408	884 : 524 890·8 : 517·2	6·8	18·3
3–13	Yellow—glaucous[a]	AB	778 : 258 3·0 : 1·0	772 : 264 2·98 : 1·02	578 : 200 : 194 : 64 579·7 : 198·3 : 192·3 : 65·7	1038	642 : 394 645·4 : 390·6	3·4	15·6
3–14	Yellow—dark axil	Ab	335 : 113 2·99 : 1·01	326 : 122 2·91 : 1·09	245 : 90 : 81 : 32 243·8 : 91·2 : 82·2 : 30·8	448	277 : 171 274·6 : 173·4	2·4	10·3
4–5	Green pod—purple	Ab	53 : 16 3·07 : 0·93	48 : 21 2·78 : 1·22	37 : 16 : 11 : 5 36·9 : 16·1 : 11·1 : 4·9	69	42 : 27 41·8 : 27·2	0·2	4·1
4–6	Green pod—stipules	AB	1156 : 368 3·03 : 0·97	1148 : 376 3·01 : 0·99	867 : 289 : 281 : 87 870·8 : 285·2 : 277·2 : 90·8	1524	954 : 570 961·6 : 562·4	7·6	18·8
4–7	Green pod—glaucous[b]	Ab	344 : 107 3·05 : 0·95	347 : 104 3·09 : 0·91	265 : 79 : 82 : 25 264·7 : 79·3 : 82·3 : 24·7	451	290 : 161 289·4 : 161·6	0·6	10·2
4–9	Green pod—colour	AB	434 : 128 3·09 : 0·91	427 : 135 3·04 : 0·96	325 : 109 : 102 : 26 329·7 : 104·3 : 97·3 : 30·7	562	351 : 211 360·4 : 201·6	9·4	11·4
4–10	Green pod—tall	AB	279 : 65 3·24 : 0·76	271 : 73 3·15 : 0·85	216 : 63 : 55 : 10 219·8 : 59·2 : 51·2 : 13·8	344	226 : 118 233·6 : 110·4	7·6	8·7
		Ab	106 : 31 3·10 : 0·90	101 : 36 2·95 : 1·05	78 : 28 : 23 : 8 78·1 : 27·9 : 22·9 : 8·1	137	86 : 51 86·2 : 50·8	0·2	5·7
		F_3	368 : 109 3·09 : 0·91	334 : 143 2·80 : 1·20	260 : 108 : 74 : 35 257·7 : 110·3 : 76·3 : 32·7	477	295 : 182 290·4 : 186·6	4·6	10·7
4–12	Green pod—fertile	Ab	189 : 44 3·24 : 0·76	165 : 68 2·83 : 1·17	130 : 59 : 35 : 9 133·8 : 55·2 : 31·2 : 12·8	233	139 : 94 146·6 : 86·4	7·6	7·4

TABLE III (*continued*).

Factor combination		Original cross	Monofactorial distribution A : a	B : b	Bifactorial distribution AB : Ab : aB : ab	Total	(AB + ab) : (Ab + aB)	Diff.	*M*
4–14	Green pod—dark axil	Ab	58 : 17 3·09 : 0·91	50 : 25 2·67 : 1·33	39 : 19 : 11 : 6 38·7 : 19·3 : 11·3 : 5·7	75	45 : 30 44·4 : 30·6	0·6	4·2
5–6	Purple—stipules	AB	176 : 52 3·09 : 0·91	168 : 60 2·95 : 1·05	150 : 26 : 18 : 34 129·7 : 46·3 : 38·3 : 13·7	228	184 : 44 143·4 : 84·6	*40·6*	7·3
		Ab	355 : 109 3·06 : 0·94	354 : 110 3·05 : 0·95	249 : 106 : 105 : 4 270·8 : 84·2 : 83·2 : 25·8	464	253 : 211 296·6 : 167·4	*43·6*	10·3
5–7	Purple—glaucous[b]	Ab	466 : 133 3·11 : 0·89	447 : 152 2·98 : 1·02	347 : 119 : 100 : 33 347·7 : 118·3 : 99·3 : 33·7	599	380 : 219 381·4 : 217·6	1·4	11·8
5–8	Purple—wing	AB	686 : 185 3·01 : 0·99	640 : 231 2·94 : 1·06	512 : 174 : 128 : 57 504·1 : 181·9 : 135·9 : 49·1	871	569 : 302 553·2 : 317·8	15·8	14·2
		Ab	298 : 99 3·00 : 1·00	310 : 87 3·12 : 0·88	237 : 61 : 73 : 26 232·7 : 65·3 : 77·3 : 21·7	397	263 : 134 254·4 : 142·6	8·6	9·6
5–9	Purple—colour	AB	649 : 211 3·02 : 0·98	860 : 291 2·99 : 1·01	649 : 211 : 291 647·8 : 212·2 : 290·9	1151 (860)	649 : 211 647·8 : 212·2	1·2	12·6
		Ab	943 : 277 3·09 : 0·91	1220 : 411 2·99 : 1·01	943 : 277 : 411 943·3 : 276·8 : 411·1	1631 (1220)	943 : 277 943·2 : 276·8	0·2	14·6
5–10	Purple—tall	AB	192 : 55 3·11 : 0·89	180 : 67 2·92 : 1·08	142 : 50 : 38 : 17 139·9 : 52·1 : 40·1 : 14·9	247	159 : 88 154·8 : 92·2	4·2	7·6
		Ab	832 : 257 3·06 : 0·94	819 : 270 2·92 : 1·08	623 : 209 : 196 : 61 625·7 : 206·3 : 193·3 : 63·7	1089	684 : 405 689·4 : 399·6	5·4	15·9
5–11	Purple—norm. stem	AB	1238 : 366 3·09 : 0·91	1228 : 376 3·06 : 0·94	938 : 300 : 290 : 76 947·8 : 290·2 : 280·2 : 85·8	1604	1014 : 590 1033·6 : 570·4	19·6	19·2
		Ab	402 : 130 3·02 : 0·98	406 : 126 3·05 : 0·95	302 : 100 : 104 : 26 306·8 : 95·2 : 99·2 : 30·8	532	328 : 204 337·6 : 194·4	9·6	11·1
5–12	Purple—fertile	AB	226 : 78 2·97 : 1·03	229 : 75 3·01 : 0·99	173 : 53 : 56 : 22 170·3 : 55·7 : 58·7 : 19·3	304	195 : 109 189·5 : 114·4	5·5	8·4
		Ab	109 : 33 3·07 : 0·93	107 : 35 3·01 : 0·99	81 : 28 : 26 : 7 82·1 : 26·9 : 24·8 : 8·1	142	88 : 54 90·2 : 51·7	2·2	5·7
5–13	Purple—glaucous[a]	Ab	432 : 127 3·09 : 0·91	419 : 140 3·00 : 1·00	320 : 112 : 99 : 28 323·8 : 108·2 : 95·2 : 31·8	559	348 : 211 355·6 : 203·4	7·6	11·4

5–14	Purple— dark axil	Ab	279 : 91 3·02 : 0·98	286 : 84 3·09 : 0·91	217 : 62 : 69 : 22 215·7 : 63·3 : 70·3 : 20·7	370	239 : 131 236·4 : 133·6	2·6	9·0
5–15	Purple— purple pod	AB	99 : 27 3·14 : 0·86	96 : 30 3·05 : 0·95	82 : 17 : 14 : 13 75·4 : 23·6 : 20·6 : 6·4	126	95 : 31 81·8 : 44·2	13·2	5·3
6–7	Stipules— glaucous[b]	Ab	574 : 195 2·99: 1·01	587 : 182 3·05: 0·95	438 : 136 : 149 : 46 438·2: 135·8 : 148·8 : 46·2	769	484 : 285 484·4: 284·6	0·4	13·4
6–8	Stipules— wing	Ab	466 : 156 3·00 : 1·00	475 : 147 3·05 : 0·95	367 : 99 : 108 : 48 355·9 : 110·1 : 119·4 : 36·9	622	415 : 207 392·8 : 229·5	22·4	12·0
6–9	Stipules— colour	AB	719 : 235 3·01 : 0·99	736 : 218 3·07 : 0·93	555 : 164 : 181 : 54 554·7 : 164·3 : 181·3 : 53·7	954	609 : 345 608·4 : 345·6	0·6	14·8
6–10	Stipules— tall	AB	255 : 89 2·97 : 1·03	271 : 73 3·15 : 0·85	203 : 52 : 68 : 21 200·9 : 54·1 : 70·1 : 18·9	344	224 : 120 219·7 : 124·2	4·2	8·9
		Ab	160 : 46 3·11 : 0·89	155 : 51 3·01 : 0·99	122 : 38 : 33 : 13 120·4 : 39·6 : 34·6 : 11·4	206	135 : 71 131·8 : 74·2	3·2	6·9
6–11	Stipules— norm. stem	Ab	589 : 195 3·01 : 0·99	638 : 146 3·26 : 0·74	484 : 105 : 154 : 41 479·3 : 109·7 : 158·7 : 36·3	784	525 : 259 515·6 : 268·4	9·4	13·2
6–12	Stipules— fertile	Ab	167 : 66 2·87 : 1·13	165 : 68 2·83 : 1·17	124 : 43 : 41 : 25 118·3 : 48·7 : 46·7 : 19·3	233	149 : 84 137·6 : 95·4	11·4	7·5
6–13	Stipules— glaucous[a]	Ab	130 : 43 3·01 : 0·99	145 : 28 3·35 : 0·65	106 : 24 : 39 : 4 108·9 : 21·1 : 36·1 : 6·9	173	110 : 63 115·8 : 57·2	5·8	6·2
6–14	Stipules— dark axil	Ab	61 : 14 3·25 : 0·75	55 : 20 2·93 : 1·07	45 : 16 : 10 : 4 44·7 : 16·3 : 10·3 : 3·7	75	49 : 26 48·4 : 26·6	0·6	4·1
6–15	Stipules— purple pod	AB	45 : 9 3·33 : 0·67	41 : 13 3·04 : 0·96	40 : 5 : 1 : 8 34·2 : 10·8 : 6·8 : 2·2	54	48 : 6 36·4 : 17·6	*11·6*	3·4
7–8	Glaucous[b]— wing	Ab	548 : 169 3·06 : 0·94	538 : 179 3·00 : 1·00	374 : 174 : 164 : 5 411·2 : 136·8 : 126·8 : 42·2	717	379 : 338 453·4 : 263·6	• *74·4*	12·9
		AB	240 : 78 3·02 : 0·98	236 : 82 2·97 : 1·03	219 : 21 : 17 : 61 178·1 : 61·9 : 57·9 : 20·1	318	280 : 38 198·2 : 119·8	*81·8*	8·6
		AB*	1067 : 1088 0·99 : 1·01	1089 : 1066 1·01 : 0·99	963 : 104 : 126 : 962 539·2 : 527·8 : 549·8 : 538·2	2155	1925 : 230 1077·4 : 1077·6	*847·6*	23·2
7–9	Glaucous[b]— colour	Ab	1406 : 444 3·03 : 0·97	1408 : 442 3·04 : 0·96	1057 : 349 : 351 : 93 1070·1 : 335·9 : 337·9 : 106·1	1850	1150 : 700 1176·2 : 673·8	26·2	20·7

TABLE III (*continued*).

	Factor combination	Original cross	Monofactorial distribution		Bifactorial distribution		Total	(AB + ab) : (Ab + aB)	Diff.	*M*
			A : a	B : b	AB : Ab	: aB : ab				
7–10	Glaucous[b]— tall	AB	1444 : 482 3·00 : 1·00	1423 : 503 2·96 : 1·04	1071 : 373 1066·9 : 377·1	: 352 : 130 : 356·1 : 125·9	1926	1201 : 725 1192·8 : 733·2	8·2	21·3
7–11	Glaucous[b]— norm. stem	AB	241 : 77 3·03 : 0·97	240 : 78 3·02 : 0·98	185 : 56 181·9 : 59·1	: 55 : 22 : 58·1 : 18·9	318	207 : 111 200·8 : 117·2	6·2	8·6
7–12	Glaucous[b]— fertile	Ab	739 : 250 2·99 : 1·01	742 : 247 3·00 : 1·00	558 : 181 554·4 : 184·6	: 184 : 66 : 187·6 : 62·4	989	624 : 365 616·8 : 372·2	7·2	15·2
7–13	Glaucous[b]— glaucous[a]	Ab	— —	— —	70 67	: 49 : 52	— —	— —	— —	— —
7–14	Glaucous[b]— dark axil	Ab	265 : 107 2·85 : 1·15	275 : 97 2·96 : 1·04	200 : 65 195·9 : 69·1	: 75 : 32 : 79·1 : 27·9	372	232 : 140 223·8 : 148·2	8·2	9·4
8–9	Wing— colour	AB	294 : 112 2·90 : 1·10	281 : 125 2·77 : 1·23	205 : 89 203·5 : 90·5	: 76 : 36 : 77·5 : 34·5	406	241 : 165 238 : 168	3·0	9·9
		Ab	819 : 275 2·99 : 1·01	819 : 275 2·99 : 1·01	613 : 206 613·1 : 205·9	: 206 : 69 : 205·9 : 69·1	1094	682 : 412 682·2 : 411·8	0·2	16·0
8–10	Wing— tall	AB	153 : 74 2·70 : 1·30	172 : 55 3·03 : 0·97	117 : 36 115·9 : 37·1	: 55 : 19 : 56·1 : 17·9	227	136 : 91 133·8 : 93·2	2·2	7·4
		Ab	592 : 224 2·90 : 1·10	597 : 219 2·93 : 1·07	452 : 140 433·1 : 158·9	: 145 : 79 : 163·9 : 60·1	816	531 : 285 493·2 : 322·8	37·8	14·0
8–11	Wing— norm. stem	AB	1124 : 357 3·04 : 0·96	1153 : 328 3·11 : 0·89	876 : 248 875·1 : 248·9	: 277 : 80 : 277·9 : 79·1	1481	956 : 525 954·2 : 526·8	1·8	18·4
8–12	Wing— fertile	Ab	136 : 50 2·92 : 0·89	140 : 46 3·01 : 0·99	104 : 32 102·4 : 33·6	: 36 : 14 : 37·6 : 12·4	186	118 : 68 114·8 : 71·2	3·2	6·6
8–13	Wing— glaucous[a]	Ab	299 : 91 3·07 : 0·93	277 : 113 2·84 : 1·16	214 : 63 212·4 : 64·6	: 85 : 28 : 86·6 : 26·4	390	242 : 148 238·8 : 151·2	3·2	9·6
8–15	Wing— purple pod	Ab	100 : 26 3·17 : 0·83	96 : 30 3·05 : 0·95	77 : 23 76·2 : 23·8	: 19 : 7 : 19·8 : 6·2	126	84 : 42 82·4 : 43·6	1·6	5·3
9–10	Colour— tall	AB	636 : 216 2·99 : 1·01	649 : 203 3·05 : 0·95	485 : 151 484·5 : 151·5	: 164 : 52 : 164·5 : 51·5	852	537 : 315 536 : 316	1·0	14·1

		Ab	1239 : 418 2·99 : 1·01	1226 : 431 2·96 : 1·04	895 : 344 : 331 : 87 916·7 : 322·3 : 309·3 : 108·7	1657	982 : 675 1025·4 : 631·6	43·4	19·8
9–11	Colour— norm. stem	Ab	1625 : 528 3·02 : 0·98	1703 : 450 3·16 : 0·84	1281 : 344 : 422 : 106 1285·4 : 339·6 : 417·6 : 110·4	2153	1387 : 766 1395 : 757·2	8·8	22·2
9–12	Colour— fertile	AB	1068 : 306 3·11 : 0·89	1037 : 337 3·02 : 0·98	810 : 258 : 227 : 79 806·1 : 261·9 : 230·9 : 75·1	1374	889 : 485 881·2 : 492·8	7·8	17·8
9–13	Colour— glaucous[a]	AB	560 : 181 3·02 : 0·98	559 : 182 3·02 : 0·98	419 : 141 : 140 : 41 422·5 : 137·5 : 136·5 : 44·5	741	460 : 281 467 : 274	7·0	13·1
9–14	Colour— dark axil	Ab	569 : 194 2·98 : 1·02	404 : 165 2·84 : 1·16	404 : 165 : 194 404·1 : 164·9 : 194·0	763 (569)	404 : 165 404·1 : 164·9	0·1	10·8
10–11	Tall— norm. stem	AB	238 : 82 2·98 : 1·02	260 : 60 3·25 : 0·75	204 : 34 : 56 : 26 193·4 : 44·6 : 66·6 : 15·4	320	230 : 90 208·8 : 111·2	21·2	8·5
		Ab	628 : 207 3·01 : 0·99	627 : 208 3·00 : 1·00	488 : 140 : 139 : 68 471·6 : 156·4 : 155·4 : 51·6	835	556 : 279 523·2 : 311·8	32·8	14·1
10–12	Tall— fertile	Ab	927 : 341 2·92 : 1·08	1055 : 213 3·33 : 0·67	785 : 142 : 270 : 71 771·3 : 155·7 : 283·7 : 57·3	1268	856 : 412 828·6 : 439·4	27·4	16·9
10–13	Tall— glaucous[a]	AB	920 : 288 3·05 : 0·95	918 : 290 3·04 : 0·96	706 : 214 : 212 : 76 699·2 : 220·8 : 218·8 : 69·2	1208	782 : 426 768·4 : 439·6	13·6	16·7
10–14	Tall— dark axil	Ab	353 : 94 3·16 : 0·84	326 : 121 2·92 : 1·08	252 : 101 : 74 : 20 257·4 : 95·6 : 68·6 : 25·4	447	272 : 175 282·8 : 164·2	10·8	10·2
11–12	Norm. stem— fertile	Ab	429 : 131 3·06 : 0·94	433 : 127 3·11 : 0·89	331 : 98 : 102 : 29 331·7 : 97·3 : 101·3 : 29·7	560	360 : 200 361·4 : 198·6	1·4	12·7
11–13	Norm. stem— glaucous[a]	Ab	637 : 189 3·08 : 0·92	653 : 173 3·16 : 0·84	510 : 127 : 143 : 46 503·6 : 133·4 : 149·4 : 39·6	826	556 : 270 543·2 : 282·8	12·8	13·6
11–14	Norm. stem— dark axil	Ab	445 : 148 3·00 : 1·00	453 : 140 3·06 : 0·94	340 : 105 : 113 : 35 339·9 : 105·1 : 113·1 : 34·9	593	375 : 218 374·8 : 218·2	0·2	11·7
11–15	Norm. stem— purple pod	Ab	124 : 43 2·97 : 1·03	132 : 35 3·16 : 0·84	95 : 29 : 37 : 6 98·1 : 25·9 : 33·9 : 9·1	167	101 : 66 107·2 : 59·8	6·2	6·2
12–13	Fertile— glaucous[a]	Ab	148 : 38 3·18 : 0·82	135 : 51 2·90 : 1·10	107 : 41 : 28 : 10 107·4 : 40·6 : 27·6 : 10·4	186	117 : 69 117·8 : 68·2	0·8	6·6
12–14	Fertile— dark axil	Ab	373 : 120 3·03 : 0·97	352 : 141 2·86 : 1·14	272 : 101 : 80 : 40 266·3 : 106·7 : 85·7 : 34·3	493	312 : 181 300·6 : 192·4	11·4	10·8

GENETIC STUDIES IN *BRASSICA OLERACEA*. II. THE KOHL RABI.

By M. S. PEASE, M.A.

(With Three Plates.)

CONTENTS.

Introduction.

The Kohl Rabi is probably one of the oldest of the cultivated varieties of *Brassica oleracea*. Though not recorded by Aristotle, Pliny describes a *Brassica* in which the stem is thin just above the roots, but swells out in the region that bears the leaves, which are few and slender. The actual passage from the *Natural History* runs: "Pompeianum procerius caule ab radice tenui, intra folia crassescit: rariora haec angustioraque, sed teneritas in dote [*est*][1]." The swollen stem and the allusion to the scanty and delicate foliage would point unmistakably to the Kohl Rabi. Nevertheless, commentators on this text and the herbalists following them, have taken Pliny's description to refer to the Cauliflower. For example, Matthiolus, who correctly describes the Kohl Rabi, goes out of his way to mention that the plant was unknown to Pliny. The Kohl Rabi figures prominently in most of the sixteenth-century herbals such as Dalechamps, who is lavish in praise of its culinary qualities, and Gerarde who states that it is grown in Italy, Spain, and Germany. In any case, whether the plant existed in classical times or not, its origin is evidently both remote and obscure. History does not throw any light on the derivation of this type, nor does it, in this case at any rate, lend support to the

[1] Translated as follows by Philemon Holland in *Plinies Naturall Historie*, Tom. II, p. 26 (London, 1601): "The Colewort Pompeianum (so called of the towne of Pompeii) is taller than the rest, rising up with a small stem from the root; howbeit among the leaves it groweth to more thicknesse."

familiar statement that all the cultivated varieties of *B. oleracea* have been produced from the wild cabbage of the seashore.

In a previous number of this *Journal* an account was given of the general problem of the genetics of *B. oleracea* and in particular attention was directed to the possibility, in certain circumstances, of "multiple linkage." Experiments on crossing cabbages were described and evidence was brought forward in support of the view that there are two multiple factors which control the character of "Heart" in the Cabbage. The present communication is intended to show that the so-called "Bulb" of the Kohl Rabi is dependent on three multiple factors, and some attempt will be made to indicate the linkage relationships between these factors and other factors which were discussed in the previous paper.

The Inheritance of "Bulb" in the Kohl Rabi.

The plants used for the original crosses in 1913 were a "blue" and a "white" Vienna Kohl Rabi (Plate XIX, figs 1 and 2). They were good specimens of their kind, with the sparse and slender foliage noticed by Pliny. By self-pollination only a few seeds were obtained and these germinated but feebly. The plants from the "blue" parent never attained a normal size, though the bulbs were true as regards shape. In the case of the "white" variety, however, the bulbs of the offspring were about normal size. In neither case did the "selfed" seed survive the five years' storage necessitated by the war; but the new Kohl Rabi parents which have since been introduced into the experiments, seem in their genetic behaviour to be similar to the original plants.

In the experiments described below, care was taken to standardise the conditions of culture from year to year, in so far as weather permitted. The seed was sown in March and the plants put out in the field as early as possible in May; the records were made in mid-winter. Under these conditions, the F_1 from the Kohl Rabi crossed by any *oleracea* type having a normal stem is in all cases clearly intermediate as regards the bulb; the structure is small and shrunken, the leaf-stalks are clustered thickly round it, and the skin is coarse and hard, like the skin of an ordinary Kale or Cabbage stem (Plate XX, figs. 7–12).

The F_2 presents the experimenter with a vast array of intermediate types of bulb. Parent forms are rare; but there is every grade of bulb from a slightly swollen stem (Plate XXI, fig. 16) to bulbs almost up to the parent size, but which somehow lack that sleek appearance, so characteristic of the structure in the parent plant (Plate XXI, fig. 15). It was not found possible to devise a method of measuring degree of "bulbness,"

which would be easily applicable to field conditions in mid-winter; and to attempt a demarcation of the various intermediate grades by eye was clearly futile. Thus only three types have been recorded, Bulb, Intermediate (or Semi-bulb), and Stalk. The plants belonging to the rare class Stalk can be picked out with confidence; but the boundary between genuine bulbs and the larger sized semi-bulbs is apt to be difficult to draw with certainty. From the nature of the material, therefore, it must be realised that an exact and critical analysis is scarcely possible. Bearing this reservation in mind, consideration may now be given to the F_2 records.

The F_2 counts for the years 1919 to 1925 are set out in Table I[1]. From this it can be seen that the ratio of the class Stalk to the total is

TABLE I.

F_2 from the cross Kohl Rabi × Normal Stalk.

Cross	Year	Reference	Bulb	Semi-bulb	Stalk	Total
Kohl Rabi × Cabbage	1919	2·15	25 (*20*)	285	9 (*5*)	319
Kohl Rabi × Curly Kale	1919	3·75	36 (*35*)	517	12 (*9*)	565
Kohl Rabi × Curly Kale	1919	4·21	14 (*11*)	164	2 (*3*)	180
Thousand-headed Kale × Kohl Rabi	1919	2·49	22 (*21*)	313	2 (*5*)	337
Kohl Rabi × Thousand-headed Kale	1919	3·1	39 (*29*)	421	6 (*7*)	466
Kohl Rabi × Cabbage	1919	2·42	8 (*6*)	79	3 (*1*)	90
Kohl Rabi × Cabbage	1920	5·18	42 (*41*)	603	13 (*10*)	658
Kohl Rabi × Curly Kale	1920	5·78	4 (*6*)	91	1 (*1*)	96
Kohl Rabi × Thousand-headed Kale	1920	5·30	20 (*20*)	286	7 (*5*)	313
Kohl Rabi × Thousand-headed Kale	1920	5·21	46 (*44*)	654	10 (*11*)	710
Kohl Rabi × Cabbage	1920	5·18	— (*3*)	44	1 (*1*)	45
Kohl Rabi × Savoy	1920	5·3	6 (*5*)	69	— (*1*)	75
Kohl Rabi × Savoy	1920	5·14	6 (*6*)	92	— (*2*)	98
Kohl Rabi × Cabbage	1920	5·45	3 (*3*)	41	1 (*1*)	45
Kohl Rabi × Curly Kale	1922	6·118	14 (*17*)	261	3 (*4*)	278
Thousand-headed Kale × Kohl Rabi	1923	7·53	3 (*9*)	143	2 (*2*)	148
Brussels Sprout × Kohl Rabi	1923	7·45	10 (*13*)	191	5 (*3*)	206
Brussels Sprout × Kohl Rabi	1923	7·122	13 (*15*)	225	7 (*4*)	245
Kohl Rabi × Brussels Sprout	1923	7·113	5 (*10*)	144	5 (*2*)	154
Kohl Rabi × Brussels Sprout	1923	7·118	5 (*8*)	122	5 (*2*)	132
Savoy × Kohl Rabi	1924	8·6	11 (*7*)	198	3 (*2*)	212
Kohl Rabi × Cabbage	1924	7·168	2 (*2*)	23	2 (—)	27
Savoy × Kohl Rabi	1925	8·101	11 (*13*)	188	1 (*3*)	200
Total observed	—	—	345	5154	100	5599
Expectation	—	—	(*350*)	(*5161*)	(*88*)	

100 : 5499, which would seem to indicate three factors, expectation on this assumption being 88 : 5511. On the other hand, by similar reasoning the ratio of the class Bulb to total, 345 : 5254, would point to two

[1] The "Reference" in this and all other tables is to the original entries in the field note-books; the number to the left of the decimal point indicates the volume and the number to the right refers to the page. The "Year" in every case refers to the year in which the culture was sown.

factors. The following hypothesis would, however, reconcile these two conclusions. It is supposed that there are three multiple factors, two of which, B_1 and B_2, are major factors, and the third, B_3, is a minor (or modifying) factor. The triple recessive represents the ordinary normal stem of the Cabbage or Kale. When both the major factors, B_1 and B_2, are present homozygously we get the familiar Kohl Rabi bulb; the minor factor B_3 may or may not be present as well, but in a plant containing the two major factors it is not possible to detect by eye the presence of the minor factor. It is only in the absence of the major factors, B_1 and B_2, that the action of the minor factor, B_3, becomes visible; for in this case it converts "Stalk" into "Semi-bulb." The hypothesis is perhaps more readily grasped when set out thus:

$$\left.\begin{array}{l} B_1B_1B_2B_2B_3B_3 \\ B_1B_1B_2B_2B_3b_3 \\ B_1B_1B_2B_2b_3b_3 \end{array}\right\} = \text{"Bulb."}$$

$$\left.\begin{array}{l} \text{All intermediate} \\ \text{combinations} \end{array}\right\} = \text{"Semi-bulb."}$$

$$b_1b_1b_2b_2b_3b_3 = \text{"Stalk."}$$

On this hypothesis the ratio of the three classes Bulb : Semi-bulb : Stalk should be as 4 : 59 : 1 and the expectation given in Table I is calculated accordingly.

A detailed examination of Table I reveals that the F_2 distributions in the crosses derived from the Brussels Sprout all show an aberration in the same sense, *i.e.* too few bulbs and too many stalks. These F_2 cultures are put together in Table II, from which it is quite clear that some other factorial scheme is at work. Evidently these F_2 cultures should be excluded from the totals given in Table I; when this is done we get a very close agreement between observation and expectation, as Table III shows.

TABLE II.

F_2. *Kohl Rabi* × *Brussels Sprout.*

Cross	Year	Reference	Bulb	Semi-bulb	Stalk	Total
Brussels Sprout × Kohl Rabi	1923	7·45	10 (*13*)	191	5 (*3*)	206
Brussels Sprout × Kohl Rabi	1923	7·122	13 (*15*)	225	7 (*4*)	245
Kohl Rabi × Brussels Sprout	1923	7·113	5 (*10*)	144	5 (*2*)	154
Kohl Rabi × Brussels Sprout	1923	7·118	5 (*8*)	122	5 (*2*)	132
Total			33	682	22	737
Expectation			(*46*)	(*680*)	(*11*)	

The expectation is calculated according to the ratio 4 : 59 : 1.

TABLE III.

Total F_2 (1919–25). Kohl Rabi × normal Stalk types other than Brussels Sprout.

	Bulb	Semi-bulb	Stalk	Total
	312	4472	78	4862
Expectation	*(304)*	*(4482)*	*(76)*	

It has been mentioned in the first of these studies (this *Journal*, vol. XVI, p. 367) that the Brussels Sprout behaves differently from other *oleracea* types when crossed with the Cabbage. It is interesting that in crossing with the Kohl Rabi, it should also give a peculiar distribution in F_2 as regards "bulbing." It is hoped to deal fully with the genetics of the Brussels Sprout in a later communication, and therefore in what immediately follows, the discussion will concern only those Kohl Rabi crosses which in F_2 seem to give the simpler and more usual distribution of types.

In dealing with a character which so conspicuously lacks sharp definition, it would be rash to attach much weight to a factorial hypothesis based on F_2 records only—more especially when it is borne in mind that the factors were so chosen that they might fit the observed facts. Corroboration is required. A good test of a multiple factor theory is offered by the Back crosses, and these have the further advantage that at the same time they should throw clear light on linkage relationships. If the hypothesis which has been outlined above holds good, then the F_1 crossed back to the Stalk, $B_1b_1B_2b_2B_3b_3 \times b_1b_1b_2b_2b_3b_3$, should give 7 semi-bulbs to 1 stalk. The converse Back cross, $F_1 \times$ Bulb,

$$B_1b_1B_2b_2B_3b_3 \times B_1B_1B_2B_2B_3B_3$$

should give 1 bulb to 3 semi-bulb. Both these Back crosses are set out in Table IV together with the respective expectations; and in both cases the test seems to bear out the theory put forward on the strength of the F_2 distribution[1]. Each Back cross was made in both directions, in order to test the possibility of the gametic ratios being different in the two sexes; but it would appear that, in this case at any rate, the precaution was unnecessary.

[1] Counts from the Back cross $F_1 \times$ Stalk made this year (1926) gave a total of 488 semi-bulbs to 68 stalks. It must, however, be put on record that this remarkably close agreement between expectation and observation in the gross figures should be to some extent discounted by the wide divergencies from expectation which occur in the five separate cultures which make up the total.

TABLE IV.

The Back crosses.

Cross	Year	Reference	Bulb	Semi-bulb	Stalk	Total
F_1 (Savoy × Kohl Rabi) × Cabbage $B_1b_1B_2b_2B_3b_3 \times b_1b_1b_2b_2b_3b_3$	1925[1]	8·153	—	488 (*489*)	71 (*70*)	559
Cabbage × F_1 (Savoy × Kohl Rabi) $b_1b_1b_2b_2b_3b_3 \times B_1b_1B_2b_2B_3b_3$	1925	9·26	—	57 (*59*)	10 (*8*)	67
Total				545 (*548*)	81 (*78*)	626
F_1 (Savoy × Kohl Rabi) × Kohl Rabi $B_1b_1B_2b_2B_3b_3 \times B_1B_1B_2B_2B_3B_3$	1924	7·172	39 (*32*)	88 (*95*)	—	127
Kohl Rabi × F_1 (Savoy × Kohl Rabi) $B_1B_1B_2B_2B_3B_3 \times B_1b_1B_2b_2B_3b_3$	1925	9·8	48 (*53*)	163 (*158*)	—	211
Total			87 (*85*)	251 (*253*)	—	338

To test the hypothesis further, there still remains the F_3 analysis, with its immense demands on time and space. In Table V is set out the behaviour expected on the three-factor theory of the 64 F_2 plants, representing the squares on an ordinary three-factor "chess board," when grown on to F_3. Only one F_2 culture, namely that from the cross Kohl Rabi by Cabbage, has been submitted to an extensive F_3 and F_4 analysis.

TABLE V.

Behaviour according to Theory of the F_2 types when grown on to F_3.

F_2 type	Number	F_3 distribution: Bulb	Semi-bulb	Stalk	Genotype (cf. Table VI)
Bulb	4	All	—	—	*A*
Semi-bulb	16	1	3	—	*B*
"	4	1	15	—	*C*
"	8	4	59	1	*D*
"	4	1	14	1	*E*
"	13	—	All	—	*F*
"	8	—	15	1	*G*
"	6	—	3	1	*H*
Stalk	1	—	—	All	*K*

These results, together with a few other cases from other crosses, are set out in Table VI and call for no special comment. It is, however, worth noticing that as regards the 22 semi-bulb F_2 plants which were tested, the numbers of each genotype found by experiment, as shown in

[1] In view of the importance of the Back crosses, it may be asked why they were not made earlier in the experiment. As a matter of fact a large number of such crosses were made in 1920, but owing to a mistaken order, all the harvest from them was lost. In the following year, the original F_1 seed, which had been grown in 1913, proved, in the most important cases, to be no longer viable; and in consequence it became necessary to start again from the beginning.

TABLE VI.

F_3 Analysis.

Original cross	F_2 Reference	F_2 Type	F_3 Reference	F_3 distribution				Genotype
				Bulb	Semi-bulb	Stalk	Total	(cf. Tab. V)
Kohl Rabi × Cabbage	5·41	Bulb	6·69	387	—	—	387	*A*
" "	5·58	"	6·68	20	—	—	20	
" "	5·41	"	7·43	100	—	—	100	
Kohl Rabi × Savoy	5·3	"	6·110	8	—	—	8	
Kohl Rabi × Curly Kale	6·119	"	7·181	63	—	—	63	
Total				578	—	—	578	
Expectation (all Bulb)								
Kohl Rabi × Cabbage	5·42	Semi-bulb	6·74	8	28	—	36	*B*
" "	5·37	"	6·54	78	220	—	298	
" "	5·53	"	6·82	11	32	—	43	
" "	5·52	"	6·73	3	7	—	10	
" "	5·19	"	6·114	2	7	—	9	
Total				102	294	—	396	
Expectation (1 : 3 : —)				*(99)*	*(297)*			
Kohl Rabi × Cabbage	5·41	Semi-bulb	6·73	2	16	—	18	*C*
" "	5·53	"	6·85	2	42	—	44	
" "	5·58	"	6·78	10	69	—	79	
" "	5·52	"	6·69	8	102	—	110	
Total				22	229	—	251	
Expectation (1 : 15 : —)				*(16)*	*(235)*			
Kohl Rabi × Cabbage	5·52	Semi-bulb	6·64	—	103	—	103	*F*
" "	5·53	"	6·84	—	20	—	20	
" "	5·59	"	6·87	—	40	—	40	
" "	5·59	"	6·80	—	18	—	18	
Kohl Rabi × Curly Kale	6·118	"	7·164	—	16	—	16	
Kohl Rabi × Curly Kale	5·78	"	6·129	—	29	—	29	
Total				—	226	—	226	
Expectation (all Semi-bulb)								
Kohl Rabi × Cabbage	5·41	Semi-bulb	6·50	—	117	10	127	*G*
" "	5·37	"	6·42	—	243	10	253	
" "	5·53	"	6·81	—	42	3	45	
" "	5·53	"	6·33	—	232	17	249	
Total				—	634	40	674	
Expectation (— : 15 : 1)					*(632)*	*(42)*		
Kohl Rabi × Cabbage	5·59	Semi-bulb	6·63	—	6	1	7	*H*
Kohl Rabi × Thousand-headed Kale	5·24	"	7·8	—	7	4	11	
" " "	5·62	"	7·52	—	89	21	110	
Total				—	102	26	128	
Expectation (— : 3 : 1)					*(96)*	*(32)*		
Kohl Rabi × Cabbage	2·16	Stalk	6·3	—	3	138	141	*K*
Kohl Rabi × Thousand-headed Kale	5·27	"	7·8	—	—	53	53	
" " "	5·32	"	7·43	—	—	80	80	
" " "	5·65	"	7·135	—	—	180	180	
Total				—	3	451	454	
Expectation (all Stalk)								
Kohl Rabi × Thousand-headed Kale	5·60	Bulb	7·6	14	34	—	48	*L*
" " "	5·76	"	7·7	5	16	—	21	
" " "	5·69	"	7·44	31	111	—	142	
Total				50	161		211	
Expectation (all Bulb)								
Kohl Rabi × Cabbage	2·20	Semi-bulb	6·15	4	257	3	264	*M*

Table VI, agree fairly well with the numbers expected, as shown in the second column of Table V. Perhaps the least reassuring feature is that the F_1 factorial combination does not clearly reappear; out of the 22 plants tested, 3 F_1 genotypes should have been expected, and in fact none was clearly found. But it must, however, be noticed that in order to distinguish with tolerable certainty between the genotypes *C*, *D*, and *E* (Tables V and VI), large cultures would be necessary. Unfortunately, not one of the four cultures which make up Section *C* of Table VI is sufficiently large to exclude the possibility of its representing in fact the F_1 distribution.

It is necessary to point out that in one case an F_2 plant recorded as stalk has given a small proportion of semi-bulbs when grown on, namely 3 out of 141 (Table VI, section *K*). It would be easy to postulate recessive bulbing factors—but for this there is no corroborative evidence. Experiments are in progress which, it is hoped, will test this point.

In section *L* of Table VI are set out three F_3 cultures from plants which were recorded as bulb, but which instead of breeding true to type, as the theory demands, have segregated into bulbs and semi-bulbs, apparently in the ratio of 1 to 3. That is to say, these F_2 plants which were recorded as bulbs have behaved as if they were semi-bulbs belonging to genotype *B*. It should be noticed that all these three plants were from one F_2 culture and were in fact grown within a few yards of each other. It is possible that they were exceptionally favourably situated and that under more normal conditions their genetic type would have become evident.

Finally, there is the case recorded in section *M* of Table VI. It is possible that this is the F_1 distribution; but the number of bulbs recorded is very low, 4 where 17 would be expected. But this culture was grown in 1921, a summer of phenomenal drought, and it is possible that in only a very few luckily situated plants did the stem swell out to the full size necessary for classification as bulb. It would be attractive to argue from this case, that the extraordinarily dry conditions of 1921 brought to light the effect of the minor factor B_3 on the other two factors B_1 and B_2. That is to say, that in the very dry weather, only the triple dominants attained the full size. But this is, of course, only a hazard. For an opportunity to put the suggestion to the test, it is necessary to await a repetition of the weather conditions of 1921.

It should perhaps be mentioned that several of the F_3 intermediate types which had bred true from F_2 were grown on to F_4 and appeared to maintain their respective types without variation (Plate XXI, figs. 17

and 18). Needless to say, both the stalks and the bulbs grown on from F_3 to F_4 all bred true.

Although the discrepancies in the F_3 analysis, which have been discussed at some considerable length, should never be lost sight of, it would seem that on the whole the F_3 analysis bears out the three-factor theory tolerably well. Further experiments may well bring to light further minor factors, or may possibly call for some revision in the definitions of the three factors; but from the experiments so far made, it may be said that the main lines of the inheritance of "bulb" in the Kohl Rabi have at any rate been clearly indicated.

THE RELATION OF THE BULB FACTORS TO THE COLOUR FACTORS D AND Δ.

It has been already noted in the previous paper that there is a colour factor D, which converts any green variety of *B. oleracea* into the corresponding purple variety. The dominance of D is pronounced and the segregation sharp. There are no doubt in some cases minor factors at work, which modify the shade and distribution of the pigment; indeed, Kristofferson has attempted a factorial analysis in such a case. But however elusive these minor factors may be, the line of cleavage between coloured and uncoloured plants determined by the factor D is clearly marked.

Several of the Kohl Rabi crosses in the experiments were heterozygous for D; the F_2 distribution from the cross Purple Kohl Rabi by two Green Stem types are set out in Table VII. It is at once evident that there is association between purple pigment and the Kohl Rabi bulb on the one hand, as against green and stalk on the other. Moreover, the five F_2 cultures in Table VII are clearly consistent between themselves and

TABLE VII.

Linkage between Colour and Bulb.
Purple, Bulb × Green, Stalk.

Cross	Year	Reference	Bulb		Semi-bulb		Stalk		Total
			Purple	Green	Purple	Green	Purple	Green	
Thousand-headed Kale × Kohl Rabi	1919	2·49	18	4	213	100	1	1	337
Kohl Rabi × Thousand-headed Kale	1919	3·1	36	3	299	122	3	3	466
Kohl Rabi × Cabbage	1919	2·15	21	4	221	64	5	4	319
Kohl Rabi × Cabbage	1920	5·18	37	5	447	156	6	7	658
Kohl Rabi × Thousand-headed Kale	1920	5·21	40	6	484	170	4	6	710
Total			152	22	1664	612	19	21	2490
Expectation for free assortment			*(117)*	*(39)*	*(1721)*	*(574)*	*(29)*	*(10)*	

TABLE VIII.

Linkage between Colour and Bulb.
Green, Bulb × Purple, Stalk.

Cross	Year	Reference	Bulb		Semi-bulb		Stalk		Total
			Purple	Green	Purple	Green	Purple	Green	
Kohl Rabi × Red Cabbage	1919	2·42	5	3	57	22	3	—	90
Kohl Rabi × Red Cabbage	1920	5·18	—	—	32	12	1	—	45
Total			5	3	89	34	4	—	135
Expectation for free assortment			*(7)*	*(2)*	*(94)*	*(31)*	*(1½)*	*(½)*	

TABLE IX.

Relation between Colour and Bulb.
F_2. *Purple Kohl Rabi × Green Stem types.*

	Bulb	Semi-bulb	Stalk	Total
Purple	152	1664	19	1835
	142	*1705*	*20*	*1867*
Green	22	612	21	655
	14	*590*	*19*	*623*
Total	174	2276	40	2490
	(156)	*(2295)*	*(39)*	

Expectation is calculated on the hypothesis that there is linkage between D and B_1 given by the gametic series $2{\cdot}3\ B_1D : 1\ B_1d : 1\ b_1D : 2{\cdot}3\ b_1d$.

justify the summation which is shown in Table IX. Set out in this form, the coupling is clearly marked. If this association of characters is due to linkage in the strict sense between the factor D and one of the B factors, then the converse cross should show repulsion where coupling was found in the first case. Unfortunately, there are only two small F_2 cultures from the cross Green Kohl Rabi by Red Cabbage. Nevertheless, the distribution of F_2 types points significantly to repulsion, as a comparison between Tables VII and VIII clearly shows. From this it would seem to be tolerably certain that linkage between D and one of the bulb factors is involved.

It now remains to determine to which B-factor D is linked, and what is the intensity of the linkage. If the coupling were between D and B_3, then the distribution of purple and green plants in the Bulb class would be normal, and the linkage would only be evident in the Stalk class. This is obviously not the case; hence D is presumably linked to one of the major factors, B_1 or B_2. And since at this stage it is quite arbitrary which of the major factors we consider to be linked to D, we may as well define B_1, as that one of the bulbing factors which is linked

to D. A determination of the intensity of this linkage can be made by writing the gametic series $xB_1D : 1B_1d : 1b_1D : xb_1d$, working out the distribution of the resulting F_2 types in terms of x, and calculating the value of x by comparison with the numbers given in Table IX. By this method, the value of x which gives the best fit is found to be $x = 2{\cdot}3$, corresponding to a crossover percentage of 30. Using this value of x, the expectation in Table IX has been calculated.

In the great majority of F_2 cultures from the cross Purple by Green *oleracea*, the familiar 3 : 1 ratio is obtained. In those, however, from the cross Purple Kohl Rabi × Green Savoy, the F_2 has consistently given 9 purple : 7 green, a ratio which points to two complementary factors being involved in the production of purple pigment. Moreover, support is given to this view by the fact that in some crosses, purple F_1 plants have been obtained from two green parents, and that these pigmented F_1 plants have given in F_2 as regards colour not a 3 : 1, but a 9 : 7 ratio. It would seem, then, that the production of purple colour in *B. oleracea* falls into line with the generally accepted notion of pigment formation in plants.

In the case of the Purple Kohl Rabi by Green Savoy crosses, the former may be supposed to contain both the pigment factors, while the Savoy has neither. If we call the second colour factor Δ, then Kohl Rabi is $DD\Delta\Delta$ and the Savoy $dd\delta\delta$. In spite of this complication, the F_2 cultures may be readily used to test the linkage between B_1 and D. The three F_2 cultures in question are set out separately in Table X, while Table XI represents the summation. From this it is clear that, while for the total F_2, a close approximation to the 9 : 7 ratio is obtained, the proportion in the Bulb class of 20 purple to 8 green is far removed from the expected ratio. The preponderance of purple bulbs over green may not unreasonably be attributed to linkage between B_1 and D, though the numbers are too small to allow of a determination of the crossover percentage.

There is, however, in this case a Back cross of sufficiently large size to warrant an evaluation of the linkage. The F_1 Kohl Rabi by Savoy was

TABLE X.

F_2. *Purple Kohl Rabi × Savoy Cabbage.*

			Bulb		Semi-bulb		Stalk		
Cross	Year	Reference	Purple	Green	Purple	Green	Purple	Green	Total
Kohl Rabi × Savoy	1920	5·14	5	1	56	36	—	—	98
Savoy × Kohl Rabi	1924	8·6	8	3	104	94	2	1	212
Savoy × Kohl Rabi	1925	8·101	7	4	98	90	—	1	200
Total			20	8	258	220	2	2	510

TABLE XI.

F_2. *Purple Kohl Rabi* × *Savoy*.
$B_1B_1B_2B_2B_3B_3DD\Delta\Delta \times b_1b_1b_2b_2b_3b_3dd\delta\delta$.

	Bulb	Semi-bulb	Stalk	Total	Expectation
Purple	20	258	2	280	*287*
Green	8	220	2	230	*223*
Total	28	478	4	510	
Expectation	(*32*)	(*470*)	(*8*)		

TABLE XII

Back Cross. F_1 (*Kohl Rabi* × *Savoy*) × *Cabbage*.
$B_1b_1B_2b_2B_3b_3Dd\Delta\delta \times b_1b_1b_2b_2b_3b_3dd\Delta\Delta$.

			Bulb		Semi-bulb		Stalk		
Cross	Year	Reference	Purple	Green	Purple	Green	Purple	Green	Total
F_1 (Savoy × Kohl Rabi) × Cabbage	1924	7·153	—	—	263	225	22	49	559
Cabbage × F_1 (Savoy × Kohl Rabi)	1925	9·26	—	—	38	19	2	8	67
Total			—	—	301	244	24	57	626

TABLE XIII.

Back Cross. F_1 (*Kohl Rabi* × *Savoy*) × *Cabbage*.
$B_1b_1B_2b_2B_3b_3Dd\Delta\delta \times b_1b_1b_2b_2b_3b_3dd\Delta\Delta$.

	Bulb	Semi-bulb	Stalk	Total	Expectation
Purple	—	301	24	325	*313*
Green	—	244	57	301	*313*
Total	—	545	81	626	
Expectation		(*547*)	(*79*)		

crossed back to an ordinary green cabbage, the pollination being made in both directions. In all the crosses made in 1923 in which this cabbage was used as a parent, the green behaved as a simple recessive to purple. As far as colour is concerned, then, this plant would seem to have been $dd\Delta\Delta$. The Back crosses in question are given in Table XII, and since they are clearly consistent amongst themselves, they have been added together and set out in Table XIII, in order to show more readily the grouping of characters. From the cross $Dd\Delta\delta \times dd\Delta\Delta$ we should expect equal numbers of purple and green, and this is in fact roughly what experiment gives (325 purple and 301 green). The crossover percentage is quite simply calculated from the distribution of colours in the Stalk class, namely $\frac{24}{24+57} = \frac{24}{81} = 30$. This happens to be exactly the number

found for this linkage from a consideration of the F_2 distribution in the other Kohl Rabi crosses which were first described (p. 263).

Thus while not too much weight should be attached to the actual value of this crossover percentage found from the F_2 and from the Back cross, it may reasonably be held that there is satisfactory evidence for the existence of linkage between the colour factor D and one of the major factors which determine the bulb of the Kohl Rabi.

THE RELATION OF THE BULB FACTORS TO OTHER FACTORS.

In the previous paper some account was given of factors affecting leaf form in *B. oleracea*. It was pointed out how unsatisfactory for exact factorial analysis were the characters under observation; that they graded one into the other, and that absolute definition was often a matter of difficulty. Nevertheless, some attempt was made to define three factors, viz. P, which determines the petiolate as against the sessile type of leaf; E, which determines entire as against lyrate; and W, which determines the broad type as distinct from the narrow. And, further, it was attempted to relate these three factors to the two factors which control the "heart" character of the Cabbage, not so much with a view to determining exact linkage values, but rather to illustrating the sort of analysis employed where linkage to a multiple factor has to be elucidated.

The data which have so far been collected for the Kohl Rabi crosses point clearly to linkage between the three factors, P, E, and W and one of the bulb factors. But at once a difficulty arises. In the case of the linkage between the colour factor D and the factor B_1, the determination of the crossover percentage has always turned primarily on the distribution of types in the rare class Bulb or in the still rarer class Stalk. In order to obtain at all reliable crossover values, clearly immense cultures are necessary, even when, as is the case in this instance, one of the characters is sharply defined. But where we are dealing with characters which lack clear definition, it would be rash to base linkage evaluations on anything but very large numbers, collected over several years, and corroborated by the corresponding F_2 and Back cross data from the converse crosses. It must suffice for the time being, therefore, to record that in the F_2 from Kohl Rabi × Cabbage there is marked association on the one hand, of the leaf characters petiolate, lyrate, and narrow with the Kohl Rabi bulb; and on the other hand, of the leaf characters sessile, entire, and broad with the normal stem type; and, further, an examination of the distribution of these characters in relation to colour seems to indicate

linkage to the factor D, and therefore, by inference, it is to the factor B_1 that P, E, and W are linked. But an exact determination of the relation of these five factors to each other must clearly await the collection of sufficiently large counts and the exploration of all the feasible tests and checks which experiment can devise.

In the previous paper it was mentioned that in the F_2 from the cross Cabbage by Kohl Rabi, there is marked association between the characters Heart and Stalk as against No Heart and Bulb. In the present paper evidence has been brought forward in support of the view that the bulb of the Kohl Rabi depends on three factors. And since we have seen that the heart is determined by two factors, the main lines of the factorial analysis of the distribution of hearts in relation to bulbs in the F_2 from the cross Kohl Rabi by Cabbage are, therefore, by now abundantly clear. Obviously the interest lies in the numerical evaluation of the linkages involved. And for this to be critical, the accumulation of adequate data must be awaited.

Summary.

(1) The swollen stem (or so-called bulb) of the Kohl Rabi is determined by three multiple factors, of which two are major and the third is a minor or modifying factor. This conclusion is arrived at from a consideration of the distribution of types in F_2, F_3, and the Back crosses.

(2) Intermediate, or Semi-bulb, types have been selected and shown to breed true.

(3) The purple colour in the "blue" Kohl Rabi is due to two complementary factors D and Δ.

(4) One of the major factors which controls the bulb in the Kohl Rabi is linked to the factor D, the crossover value being 30 per cent.

I am deeply beholden to Prof. Sir Rowland Biffen, who has provided most generous accommodation for these experiments at the Cambridge University Plant Breeding Institute.

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Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 11.

Fig. 12.

Fig. 13.

Fig. 14.

Fig. 15.

Fig. 16.

Fig 17.

Fig. 18.

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EXPLANATION OF PLATES.

PLATE XIX. Parent types.

Fig. 1. Blue Vienna Kohl Rabi.
Fig. 2. White Vienna Kohl Rabi.
Fig. 3. Savoy Cabbage.
Fig. 4. Thousand-headed Kale.
Fig. 5. Drumhead Cabbage.
Fig. 6. Curly Kale.

PLATE XX. F_1 Types.

Fig. 7. Kohl Rabi × Thousand-headed Kale.
Fig. 8. Kohl Rabi × Broccoli.
Fig. 9. Kohl Rabi × Cabbage.
Fig. 10. Kohl Rabi × Savoy Cabbage.
Fig. 11. Kohl Rabi × Curly Kale.
Fig. 12. Kohl Rabi × Brussels Sprout.

PLATE XXI. F_2 and F_4 types from the cross Kohl Rabi × Cabbage.

Fig. 13. F_2. Kohl Rabi type.
Fig. 14. F_2. Cabbage type.
Fig. 15. F_2. Semi-bulb (towards Bulb) type.
Fig. 16. F_2. Semi-bulb (towards Stalk) type.
Fig. 17. F_4. A true breeding Semi-bulb type.
Fig. 18. F_4. Another true breeding Semi-bulb type.

THE INFLUENCE OF *POLLEN MATURITY* AND *RESTRICTED POLLINATION* ON A SIMPLE MENDELIAN RATIO IN THE PEA.

By C. J. BOND, C.M.G.

(With Four Text-figures.)

In this communication I propose to record some of the results which have been obtained in experiments carried out during the last twelve years, to ascertain whether seeds obtained after pollination of the immature stigma of the unopened bud vary in genetic constitution from seeds obtained by pollination of the mature stigma of the fully opened flower in the hybrid pea.

I shall also describe certain other experiments designed to throw light on the influence exerted on seed character by artificial pollination with a restricted or "minimal" amount of pollen, and finally the place of the individual seed in the pod, and the position of the pod on its stem in relation to seed characters, to stage of growth, and reproductive activity of the parent plant.

In regard to the first point—pollination of the unopened bud and the fully opened flower—12 F_1 hybrid plants from a cross between Early Sunrise (a round yellow seed pea) and Little Marvel (a wrinkled green seed pea) were used.

Of these hybrid plants 20 flower buds were castrated in the young, unopened stage, and mature pollen from other flowers of the same plant was deposited in full quantity on the immature stigma of the young unopened bud, at the time of the removal of the anthers.

A corresponding number of other flowers on the same plants were allowed to undergo natural self-fertilisation, at the normal stage of full development of the stigma in the fully opened flower.

The seeds from these latter pods were used as controls.

From the flowers pollinated artificially in the immature or bud stage 20 ripe pods were obtained, containing 105 seeds.

The following represents the constitution of these seeds, as determined later when fully ripe.

Bud Pollination, 105 seeds:

Round yellow	55
Wrinkled yellow	23
Round green	14
Wrinkled green	13
	105

Open Flower Pollination (20 pods containing 104 seeds from the naturally fertilised open flowers) gave:

Round yellow	70
Wrinkled yellow	10
Round green	22
Wrinkled green	2
	104

Comparing seed colour in the two series we get:

Bud Poll.: 1 green to (just under) 3 yellow.
O. F. Poll.: 1 green to (just over) 3 yellow.

Seed Shape:

Bud Poll.: 1 wrinkled to 2 round.
O. F. Poll.: 1 wrinkled to nearly 8 round.

If we compare combined colour-character we get a ratio of:

Bud Poll.: 1 wrinkled yellow to $2\frac{1}{3}$ round yellow.
O. F. Poll.: 1 wrinkled yellow to 7 round yellow.

Combined seed shape characters:

Bud Poll.: 1 wrinkled green to 4 round yellow.
O. F. Poll.: 1 wrinkled green to 11 round yellow.

Thus, with the exception of greens to yellows which show only a slight difference, we find an increased proportion of recessive characters in the seeds of the bud pollination over those of the O. F. pollination series.

If we go into further detail and compare the characters of each seed in the 20 pods in the two series we find that in

Seed 1, or the apical seed (in 20 pods),

in the Bud Poll. series is:

R. Y. in	9	pods
W. Y. in	6	,,
R. G. in	4	,,
W. G. in	1	,,
	20	

in the F. F. Poll. series is:

R. Y. in	13	pods
W. Y. in	2	,,
R. G. in	5	,,
W. G. in	0	,,
	20	

Total green to yellow: Bud Poll. 5 G. to 15 Y.
O. F. Poll. 5 G. to 15 Y.

Total wrinkled to round: Bud Poll. 7 W. to 13 R.
O. F. Poll. 2 W. to 18 R.

Seed 2,

in the Bud Poll. series is:

R. Y. in	11	pods
W. Y. in	1	,,
R. G. in	4	,,
W. G. in	4	,,
	20	

in the O. F. Poll. series is:

R. Y. in	12	pods
W. Y. in	1	,,
R. G. in	7	,,
W. G. in	0	,,
	20	

Total green to yellow: Bud Poll. 8 G. to 12 Y.
O. F. Poll. 7 G. to 13 Y.

Total wrinkled to round: Bud Poll. 5 W. to 15 R.
O. F. Poll. 1 W. to 19 R.

Seed 3,

in the Bud. Poll series is:

R. Y. in	9	pods
W. Y. in	6	,,
R. G. in	0	,,
W. G. in	5	,,
	20	

in the O. F. Poll. series is:

R. Y. in	14	pods
W. Y. in	3	,,
R. G. in	2	,,
W. G. in	1	,,
	20	

Total green to yellow: Bud Poll. 5 G. to 15 Y.
O. F. Poll. 3 G. to 17 Y.

Total wrinkled to round: Bud Poll. 11 W. to 9 R.
O. F. Poll. 4 W. to 16 R.

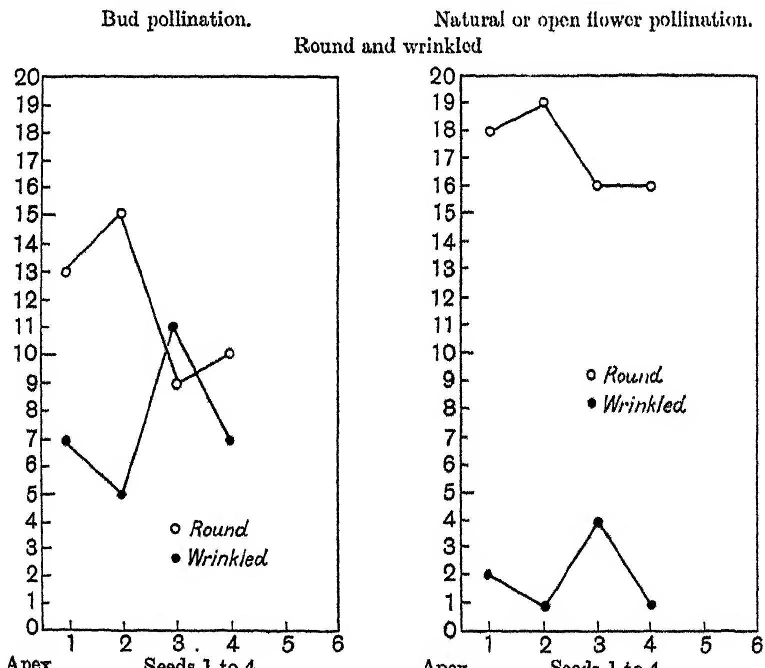
Seed 4 (in comparing the 4th seed it is necessary to exclude 2 pods of 3 seeds only in the bud, and 1 pod of 3 seeds in the O. F. series, thus making 17 pods),

in the Bud Poll. series is:		in the O. F. Poll. series is:	
R. Y. in	7 pods	R. Y. in	14 pods
W. Y. in	7 ,,	W. Y. in	1 ,,
R. G. in	3 ,,	R. G. in	2 ,,
W. G. in	0 ,,	W. G. in	0 ,,
	17		17

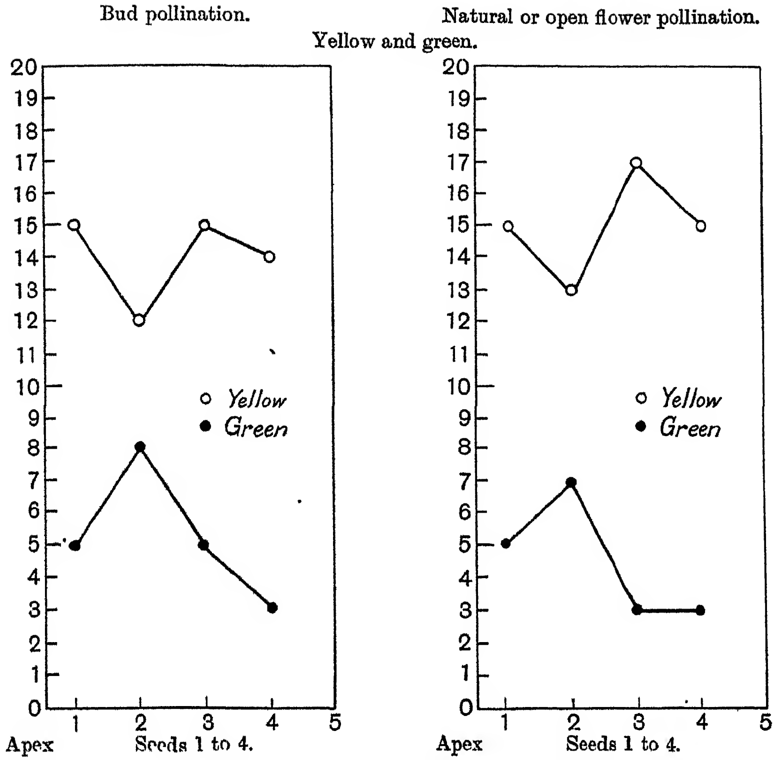
Total green to yellow: Bud Poll. 3 G. to 14 Y.
O. F. Poll. 2 G. to 15 Y.

Total wrinkled to round: Bud Poll. 7 W. to 10 R.
O. F. Poll. 1 W. to 16 R.

These results can be recorded graphically in the following graphs, which show the proportion of dominant and recessive characters in the seeds in relation to their position in the pod.



Graph 1. E. Sunrise poll. L. Marvel F_1 selfed.



Graph 2. E. Sunrise poll. L. Marvel F_1 selfed.

Thus, when we compare corresponding seeds in corresponding positions in the pod, from apex to base, in the two series, although in the case of seed *colour* the difference is not marked, yet in the case of seed *shape* the bud series has a majority over the O. F. series of wrinkled over round in all seeds from the 1st to the 4th, while the O. F. series has a corresponding preponderance of round seeds. This difference is less noticeable in the 5th and 6th seeds.

It seems therefore that difference in seed shape is most marked in the seeds in the middle of the pod. It reaches its maximum in the 3rd seed, where there is an absolute majority of wrinkled over round in the bud pollinated series. If pollen tubes from pollen grains of different genetic composition vary in capacity and rate of growth, then the length of route which has to be traversed by a pollen tube may exercise an important selective influence over the fertilising capacity of different male nuclei when they reach the ovules.

But the further question arises: Why should pollination of the young, undeveloped stigma by mature pollen (immature pollen from unbroken anthers will not adhere to the stigma) from the same or another flower of the same plant give an excess of recessive characters in the seeds?

Is it because the pollen grains remain inactive on the stigma for several days before any growth of the pollen tubes takes place, and that during this interval they pass through changes which favour a preferential activity on the part of the recessive character-bearing grains?

Or does the delay in the activity of the pollen grains (in association with immaturity of the stigma and ovules) bring about some selective form of fertilisation, whereby recessive character-bearing pollen tubes unite with recessive character-bearing ovules in greater proportion than normal?

A bud pollinated in the unopened, immature stage goes on developing and does not fully open for from four to five days after the removal of the anthers and artificial pollination.

If the pollen tubes do not commence to penetrate the style till the bud is fully opened and the stigma is mature, then this delayed activity of the pollen tubes would account for the greater age of the male nuclei on reaching the ovules in the bud-pollinated as against the O. F. series.

In regard to this point Parnell (*Journ. Genetics*, Vol. XI, No. 3) has shown that the pollen grains of rice vary in their starch content and form two types of seed, a starchy and a glutinous type. Professor Punnett has suggested to me that if the pollen grains of the pea differ in their starchy material in the same way, there may be an association between the starch character and the rate of growth of the pollen tubes, which might explain the interference with the normal ratio in seed character in the bud pollinated, *i.e.* the delayed fertilisation series.

Sears and Metcalf (*Journ. Genetics*, Vol. XVII. No. 1), in dealing with the behaviour of pollen starch in a geranium and its bud sport, point out that the pollen of the open flowers of the salmon-fringed pelargonium has double the percentage of starch-filled grains compared with the pollen of its zonal bud sport. They also point to the value of carbohydrate analysis of pollen for genetical purposes, and give references to other papers on pollen dimorphism in maize and other plants.

It may also be that delayed fertilisation, together with restricted pollination, may account for the "aberrant cases" in Darbishire's results; see paper by Udny Yule (*Journ. Genetics*, vol. XIII. No. 3).

Maximal and Minimal Pollination.

The second condition at the time of fertilisation which may influence the proportion of dominant and recessive characters in the F_1 seeds is that of the numerical proportion of functionally active pollen grains which reach the stigma during the fertilisable stage of its growth.

I have already recorded observations (see *Journ. Genetics*, Vol. IV. April 1915) on female *Lychnis* flowers, which show that in order to ensure the continued growth of the ovary and its contained ovules, and in order to prevent the falling of the flower by absorption of the cells at the base of the thalamus, a sufficient number of ovules (more than six in the case of the *Lychnis* flower) must undergo adequate fertilisation and must continue to develop.

This means that more than six pollen grains must reach the stigma at the appropriate period.

The ripe *Lychnis* capsule, after adequate fertilisation, normally contains some hundreds of seeds. By "*minimal*" pollination is meant the application of pollen grains insufficient in numbers to fertilise more than a very small proportion of the ovules present, and by "*maximal*" pollination is meant a supply of pollen grains in excess of the number of ovules.

On this subject see Von Correns, "Über den Einfluss des Alters der Keimzellen, I." *Sitzber. Preuss. Akad. Wiss.* 1924.

There is some evidence in the case of the Pea (the Early Sunrise and Little Marvel cross) that pods containing normal seeds cannot be obtained unless the number of pollen grains exceeds 20 to 25, though in this variety the average number of seeds in the pod is 5 or 6.

The method adopted has been to collect a quantity of pollen on some smooth steel instrument, a blunt surgical cataract knife or blunt needle, and then, with the help of a watchmaker's glass, to shake or blow away the grains till the requisite number remains. These are then gently transferred to the stigma of the previously castrated and suitably protected flower.

We must now discuss the different effects produced by maximal and minimal pollination respectively on the proportion of dominant to recessive characters shown by the seeds in the case of the heterozygous pea, or the seedling plants in cases where the seeds themselves do not, like the pea, indicate at once their genetic composition.

A considerable number of experiments have been carried out during the last ten years to throw light on this problem. Some of these have

been somewhat indeterminate, and have indicated that other variable factors may have influenced the result. One such factor probably is the choice of the ovule-bearing and the pollen-bearing parent plant in each experiment.

For instance, the increase in recessive character-bearing seeds was more marked in crosses in which the recessive plant was the ovule-bearing and not the pollen-bearing parent.

The following table gives in summary the results of a series of experiments on about 300 seeds:

Hybrid Pea (Early Sunrise, Y. R., poll. Little Marvel, G. W. F_1 selfed).

Minimal Poll.			*Maximal Poll.*		
Seed shape:	Round	70·5 %	Seed shape:	Round	72·9 %
	Wrinkled	29·2		Wrinkled	27·1
Seed colour:	Green	24·5	Seed colour:	Green	21·4
	Yellow	75·5		Yellow	78·6

The total number of seeds being 212 in the minimal and 350 in the maximal series.

Further experiments were tried with another cross: Prince of Wales (wrinkled yellow) with Telegraph (green, round).

In all these, with the exception of one series, a relative majority of wrinkled over round seeds was obtained in the *minimally* pollinated series, together with a relative majority of greens over yellows in the same series.

From these results, although the numbers are few, it is, I think, clear, that (at any rate in this cross) *minimal* pollination tends to increase the proportion of seeds bearing recessive, to seeds bearing dominant characters in flowers so pollinated as compared with the seeds in other flowers in which the available pollen grains have been largely in excess of the number of ovules to be fertilised.

It is at present too soon to decide definitely as to the way in which *minimal* pollination produces this result.

The experiments on the *Lychnis* flowers have shown that the first demand on the available pollen supply is made by the ovules at the apex of the ovary; that is, by the ovules nearest to the style, the route by which the pollen tubes reach the ovules.

These apical ovules are the only ones to develop in cases of a *very* restricted pollination in the *Lychnis* ovary.

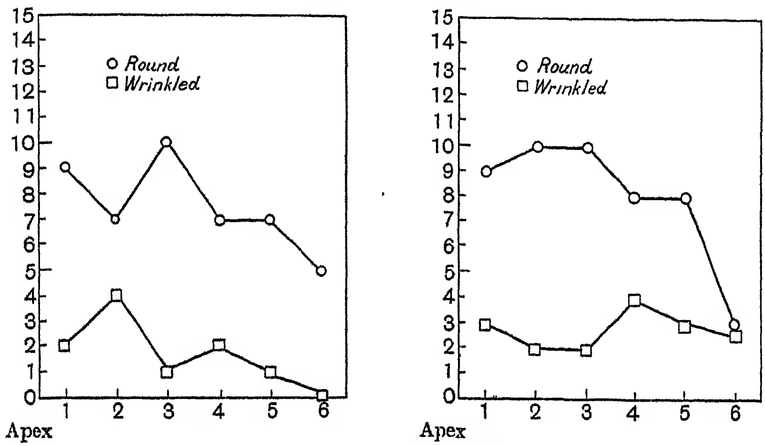
The question arises whether differences in genetic composition are

originally present in the ovules at the apex as compared with those at the base of the pod in the pea; or whether the effect is due wholly to pollen differences.

On this point the facts given previously when discussing the relative proportion of recessive and dominant characters in corresponding seeds

Minimal pollination. *Maximal* pollination.

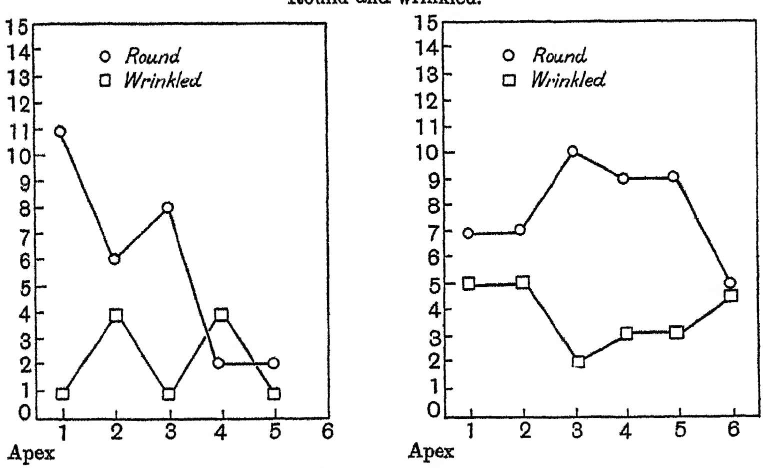
Round and wrinkled.



Graph 3. Telegraph poll. Prince of Wales F_1 selfed.

Minimal pollination. *Maximal* pollination.

Round and wrinkled.



Graph 4. Prince of Wales poll. Telegraph F_1 selfed.

in the pods of the "bud pollinated" and the "open flower" pollinated series respectively are of interest.

There we found that the difference in regard to seed shape (round and wrinkled) was more marked in seeds in the middle of the pod[1], rather than the apex, that is, in the situation requiring a longer growth of pollen tubes; in other words, while differences in genetic character are more marked in the seeds in the middle of the pod in pollination of the immature stigma, in *minimal* pollination the effect falls chiefly on the *apical*, especially the second seed.

These results are shown in Graphs 3 and 4.

Microscopical sections of different styles at different intervals after pollination, with young and old, and with homozygous and heterozygous pollen grains, would probably throw an important light on the rate of growth of pollen grains of different degrees of maturity, and of different genetical composition, as judged by different dates of arrival at the ovules.

Experiments might also be undertaken to test the proportion of dominant and recessive seeds which follows the pollination of ovules by recently matured pollen, and by pollen that has been stored for some days before use.

Position of the Pods on the Plant Stem.

The third and last condition which may exert some influence on the proportion between recessive and dominant seeds has reference to the position of the pods on the stem of the plant in relation to age and flowering activity.

The pea plant (*Pisum sativum*) varies in its type of growth. Some plants have a single stem with pods arranged singly or in pairs in an alternating series on opposite sides of the stem. Other plants have one primary stem, from which at intervals secondary stems arise, each with its alternating series of pods.

It is necessary therefore in carrying out observations on the seeds in different pods to select plants of the single-stem type, or to treat the secondary stems with their alternating series of pods as individual plants for the present purpose.

Bearing this in mind the records from two series of experiments on heterozygous pea plants with pods containing seeds of clearly recognisable dominant and recessive characters, show a difference in ratio according

[1] By middle of the pod is meant the site of the third and fourth seeds counting from the apex.

as the plant with dominant characters formed the pollen or the ovule parent. This means that the question of the reverse cross has also to be considered.

In 14 plants (Prince of Wales pollinated Little Marvel, F_1 selfed naturally) the proportion of green to yellow seeds was

Among 59 seeds in the apical pods of the 14 plants: 1 G. to $2\frac{1}{6}$ Y.
Among 88 seeds in the basal pods of the 14 plants: 1 G. to $3\frac{1}{2}$ Y.
In the middle pods[1] of the 14 plants: 1 G. to 4 Y.

In an earlier and larger series (Prince of Wales pollinated Telegraph cross) the proportion was in 20 plants:

In the apical pods: 1 G. to $3\frac{1}{2}$ Y.
In the basal pods: 1 G. to 5 Y.

While in the reverse cross (Telegraph pollinated Prince of Wales) the proportion was in 12 plants:

In the apical pods: 1 G. to $2\frac{1}{2}$ Y.
In the basal pods: 1 G. to $2\frac{1}{3}$ Y.

whereas with seed shape the proportion was in the Prince of Wales pollinated Telegraph cross:

In the apical pods: 1 wrinkled to 7 round
In the basal pods: 1 wrinkled to 3 round

and in the reverse cross (Telegraph pollinated Prince of Wales):

In the apical pods: 1 W. to 11 R.
In the basal pods: 1 W. to 2 R.

Although the number of pods and plants examined is small in the first series, the result suggests that the proportion of green to yellow remains fairly level in the seeds in the lower pods, green falls a little in the middle pods (perhaps at the stage of greatest reproductive activity), and rises again to a maximum in the apical pods when reproductive vigour is beginning to decline.

In the second series (Prince of Wales pollinated Telegraph) a like result is shown, namely, a rise in the proportion of green to yellow from 1 G. to 5 Y. in the bottom pods, to 1 G. to $2\frac{1}{2}$ Y. in the top pods. The reverse cross shows, however, practical equality between the upper and lower pods.

Seed shape in the second series gives the opposite condition, namely, 1 wrinkled to 7 round in the top, to 1 wrinkled and 3 round in the

[1] In the case of middle pods one central pod was taken in plants of 3 and 5 pods and the two middle pods in plants with 5 pods.

bottom pods; and in the reverse cross, 1 wrinkled to 11 round in the top, and 1 wrinkled to 2 round in the bottom pods.

Reference should here be made to a paper by the late W. Bateson and Caroline Pellew on "The Genetics of Rogues among Culinary Peas" (*Journ. Genetics*, Vol. v. No. 1), in which the suggestion is made that the disappearance of the type elements in the F_1 intermediates (Type crossed with Rogue) is due to the fact that such elements, being introduced from one side only of the parentage, are used up and cut out of the germ lineage in the early stages of somatic development.

The experiments now recorded on the genetic characters shown by the seeds in the apical, middle, and lower pods respectively of the same plant, also suggest an influence exerted by a differentiating division of somatic cells, in favouring certain genetic characters over others, in the seeds subsequently formed.

Summary.

In summing up the evidence recorded in the foregoing observations and in attempting to compare the effect on the relative proportion of dominant to recessive characters in seeds which have been subjected to altered conditions during growth and fertilisation, conditions described under the three headings (1) genetic maturity, (2) minimal pollination, and (3) serial order of pod production, one or two facts seem to emerge which may be of importance in pointing the way to further investigations on a larger scale.

The first is that pollination of the immature stigma in the unopened bud leads to a lengthening of the interval between the deposition of the pollen on the stigma and fertilisation of the ovules.

This delay in fertilisation of the ovules by "ageing" pollen grains, leads to an increased proportion of seeds with recessive, to seeds with dominant characters among the ovules fertilised under such conditions.

In view of previous work by Parnell, Sears and Metcalf, and other observers, it seems probable that differences in the nature of the starch content of pollen grains of different genetic constitution may be associated with different rates of development, and that pollen grains with wrinkled starch may be more capable of withstanding the delay in fertilisation which occurs in the bud pollinated series than pollen grains with round starch.

"Minimal pollination"—that is the deposition of pollen grains on the stigma in greatly reduced numbers, far below the numbers present under normal conditions of self-fertilisation—also seems to be generally

associated with an increase in the ratio of recessive character-bearing to dominant character-bearing seeds from ovules so fertilised.

It is not yet possible to say whether this result is due to preferential, *i.e.* selective, fertilisation between the pollen tubes and ovules of similar genetic character, or to some form of selective mortality among the ovules themselves.

Bearing in mind also the important changes which take place in the cells of the peduncle of the ovarian thalamus in the fully pollinated *Lychnis* flower with adequately fertilised ovules, one effect of a greatly reduced number of pollen grains reaching the ovary may be to bring about some disturbance in the chemical or hormonic influences which cause the rapid growth of ovarian tissue in the one case, or the flower to fall prematurely in the other.

Although the evidence is not so clear in the case of the serial position of pods on the stem of the plant, and although this requires further investigation on a larger scale, there is yet some reason to think that the proportion of dominant character-bearing to recessive character-bearing ovules varies according to the stage of reproductive activity of the plant at the time the ovules are produced. Thus in most cases the tendency is for the recessive gametes to show an increase in number over the dominant gametes at the later or declining stages of plant growth and flower production, that is, in the later formed pods at the summit of the stem, as compared with the earlier formed pods at the base.

If further experiments should show that these differences do arise in the gametes (male or female or both) under these varying growth conditions, then this fact must affect the statistical data obtained from the collection of seeds from different parts of the plant, as far as numerical proportions of a Mendelian kind are concerned.

PREPONDERANCE OF *DICOCCUM*-LIKE CHARACTERS AND CHROMOSOME NUMBERS IN HYBRIDS BETWEEN *TRITICUM DICOCCUM* AND *TRITICUM VULGARE*[1].

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CONTENTS.

1. Historical Introduction.

The gametic chromosome number of the Emmer series of wheats is 14, and that of the *vulgare* series is 21 (Kihara (3); Sax (6)). In crosses between members of the two series, the F_1 has a somatic number of 35, the sum of the gametic numbers. At the heterotypic division 14 bivalent chromosomes and 7 univalents appear, the 14 Emmer chromosomes having presumably mated with 14 of the *vulgare* ones, leaving 7 unpaired. The bivalents behave normally at both divisions; the univalents, after lagging behind the others, divide at the first division, but at the second remain undivided and wander tardily to the poles. They apparently segregate at random and the resulting gametes therefore have 14 to 21 chromosomes, the great majority having intermediate numbers.

[1] This investigation has been carried on with the aid of a grant from the National Research Council of Canada.

Several investigators have reported the frequencies of the different somatic numbers between 28 and 42 in F_2 and later generations of crosses between members of the two series. A much larger proportion have numbers approaching those of the parents than would be expected. Sax (7) and Thompson (8) found most F_2 and F_3 segregates of *durum* × *vulgare* crosses with haploid numbers of 14 or 21. Both report the number of plants approaching the *durum* condition greater than the number approaching the *vulgare* condition. Kihara (4), on the other hand, in a number of crosses found the majority to be more *vulgare*-like in chromosome number.

Correlation of characters, and of characters with chromosome numbers has been reported. Hayes, Parker and Kurtzweil (2) found correlation of rust-resistance and *durum* characters in segregates of *durum* × *vulgare* crosses. Sax (7) reported for F_3 segregates of the same cross correlation between the 21-chromosome condition and a few *vulgare* characters on the one hand, and between the 14-chromosome condition and a few *durum* characters on the other. Kihara (4) reports that the 14-chromosome segregate resembles the Emmer type parent in some respects and that the 42-chromosome segregate resembles the *vulgare* type. Thompson (8) studied numerous distinctive characteristics in F_2 segregates of a *durum* × *vulgare* cross in an attempt to prove or disprove correlation between the whole series of *durum* or *vulgare* characters and found a high degree of correlation for each set. Few plants in comparison with Mendelian expectations had approximately equal numbers of *durum* and *vulgare* characters, but many more had this condition, along with an intermediate chromosome number, than Sax reported for F_3 segregates of the same cross. There was correlation between the respective chromosome numbers and parental characters. This correlation was not absolute, some 14-chromosome plants having one or few *vulgare* characters, and some 21-chromosome plants having a few *durum* characters.

Hayes, Parker and Kurtzweil investigated a few characters of F_2 and F_3 segregates of cross between *T. vulgare* and *T. dicoccum*. They report correlation between *dicoccum* characters and rust resistance. The difference between *dicoccum* and *vulgare* is greater than between *durum* and *vulgare*, *dicoccum* having such distinctive characters as a disarticulating rachis and closely adherent glumes.

Hitherto no examination has been reported of the cytological behaviour of *dicoccum* × *vulgare* hybrids. The results of such a study are given in the following pages, together with the results of a correlated

genetic study of the same plants. Both the genetic and cytological studies have revealed important differences between the *dicoccum* × *vulgare* cross and crosses of *vulgare* with other 14-chromosome wheats.

2. MATERIALS AND METHODS.

In the investigations described in this paper the *dicoccum* (Emmer) parent belonged to the variety *farrum*, according to Percival's classification (5), and the *vulgare* parent was Marquis. The *durum* × *vulgare* data given for comparison were obtained from hybrids between Iumillo and Marquis, which Thompson used in securing the results mentioned above on correlation of characters.

In most cases the chromosomes were studied by the Belling (1) method. The fresh anthers were used at once, or were fixed in Carnoy's fluid, run gradually into 70 per cent. alcohol, and preserved in the latter until used. In other cases they were studied from portions of the ear fixed in Carnoy's fluid, run into paraffin, sectioned and stained with Haidenhain's haematoxylin. The use of Belling's solution on preserved material proved quite satisfactory and has several advantages over the paraffin method.

3. CYTOLOGICAL RESULTS IN F_2 AND F_3 SEGREGATES.

An attempt was made in each case to ascertain the numbers of bivalents and univalents. Satisfactory results were obtained for most plants for which counts of the total number were secured. In several cases the number of bivalents was obtained by subtracting the greatest number of lagging chromosomes seen at the heterotypic anaphase from the total number, since sometimes the univalents could not be distinguished from bivalents with certainty by their position or shape in polar views. In most instances it was possible to identify the univalents at the metaphase, especially if the number was small.

Table I shows the frequency of the various combinations of bivalents and univalents in the 28 F_2 plants for which counts were obtained. The last column shows the numbers of plants having 14, 15, etc., bivalents without reference to univalents.

TABLE I.

Frequencies of chromosome combinations in 28 F_2 segregates.

	Univalents								Total number of plants
Bivalents	0	1	2	3	4	5	6	7	
14	6	7	5	4	2				24
15					1		2		3
16					—				—
17				1					1

It will be seen that the great majority of the plants had 14 bivalents and few univalents or none at all. Only 4 plants had more than 14 bivalents and of these 1 had 14 or 15, 2 had 15, and 1 had 17. There were no plants with more than 17 bivalents and only 2 with 21 univalents and bivalents combined. The absence of any numbers approaching the 21 bivalents of *vulgare* is very striking, and in contrast with results reported for F_2 and more frequently for later generations of other crosses between 14- and 21-chromosome wheats.

It has been noted above that with random segregation of univalents at the homotypic division most of the F_1 gametes would have chromosome numbers intermediate between 14 and 21. The univalents lagging behind the bivalents may fail to be reconstituted in the reforming nuclei in either division. This chromosome loss reduces somewhat the proportion of gametes with higher chromosome numbers, and so makes those with intermediate numbers greater.

Disregarding chromosome loss and assuming complete gametic and zygotic fertility, a random meeting of F_1 gametes would give the chromosome frequencies for F_2 as shown in Table II. The table gives in addition the actual frequencies of somatic numbers in the 28 F_2 plants, as recorded in Table I, and those obtained by Kihara and Sax from F_2 segregates of various crosses between 14- and 21-chromosome wheats.

TABLE II.

Frequencies of chromosome numbers in F_2.

	Chromosome number														
	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Expected	1	14	91	364	1001	2002	3003	3432	3003	2002	1001	364	91	14	1
Vulgare-dicoccum	6	7	5	4	2	—	1	—	2	1	—	—	—	—	—
Vulgare-polonicum (Sax)	5	—	—	—	1	—	1	5	2	—	—	—	—	—	1
Several crosses (Kihara)	—	—	1	1	1	1	—	1	1	2	8	2	1	—	1

The expected and actual frequencies in *vulgare* × *dicoccum* segregates present a remarkable contrast. The expected frequency for 28 chromosome plants is 1 in 16,384, the actual is 6 in 28. There is a concentration of individuals toward the 28-chromosome end of the table instead of in the middle. In a small group all would be expected to be intermediate; actually few have this condition.

Of the other results Kihara's are the only ones which approach the expected and they are from several very small groups. He states that the existence of F_2 segregates with the missing numbers cannot be doubted.

Sax's results with F_3 and Thompson's with F_2 of *durum* × *vulgare* agree in showing that most plants had parental or near-parental conditions, though Thompson's included a much higher proportion of intermediates. This is partly accounted for by the fact that F_2 intermediates are less fertile than the others (8). Both writers find the number of plants with *durum* or near-*durum* chromosome conditions greater than those with *vulgare* or near-*vulgare* conditions.

The results from the 28 *vulgare* × *dicoccum* F_2 segregates examined are in accord with those of Thompson for *vulgare* × *durum* in having many 14- and 15-chromosome plants. The proportion of intermediates in *vulgare* × *dicoccum* was about the same as in *vulgare* × *durum*. While many *vulgare* × *durum* segregates had 20 or 21 chromosomes, few *vulgare* × *dicoccum* ones had these high numbers. The highest somatic number found was 37, and only 3 plants had more than 34. In the much larger proportion of low-chromosome plants they show a more intensified effect of some factor which tends to reduce the chromosome number to that of the 14-chromosome parent.

Material from a few F_3 plants of three families was preserved for cytological study and the frequencies of different chromosome combinations in 9 of these plants is recorded in Table III. All had 14 bivalents. This is not significant in itself as only three families are represented, but as far as it goes it confirms the findings in F_2.

TABLE III.

Frequencies of chromosome combinations in 9 F_3 segregates.

Bivalents	Univalents 0	1	2	3	4	5	6	7
14	4	4		1				

From Table VIII (p. 295) where 10 F_3 plants are grouped in families, it will be seen that 9 of these are from two families and the tenth from a third. These 9 have chromosome numbers of 14 or 15 (with one possible exception). It is likely that the parent in each case had 29 chromosomes producing 14- or 15-chromosome gametes depending on the absence or presence of the one univalent. No conclusion as to the chromosome condition of the parent of the 17-chromosome segregate can be reached except that it had 14 bivalents and a number of univalents. If the supposition as to parental conditions in the other two families is correct, it is significant that no plants with 15 bivalents were found. They should occur as frequently as those with 14 bivalents,

unless the univalent was lost, or unless plants with 15 pairs are not viable.

From a study of chromosome numbers found in F_2 and succeeding generations of crosses between 14- and 21-chromosome wheats Kihara (4) found that the plants fell into three groups according to relationships of bivalents and univalents. All his plants with less than 35 chromosomes had only 14 bivalents. These he called the "decrease group" because they approached the 28-chromosome condition in succeeding generations. In most of the others the sum of the bivalents and univalents was 21, showing that at least one complete set of the extra 7 *vulgare* chromosomes was present. These made up his "increase group" and they approached the 42-chromosome condition in succeeding generations. A few others which did not conform to this classification, having for instance 20 bivalents and no univalents, he called "sterile combinations" because they were usually dwarf and set no seeds or a few which germinated poorly or not at all. Taking all his crosses together, in none of which *dicoccum* was used, he found 16 in the "decrease" group, 19 in the "increase" group and 2 "sterile combinations."

Reference to Table I shows that the proportions in our *dicoccum* × *vulgare* cross are very different: 24 would belong to Kihara's decrease group, 2 (those with 15 bivalents and 6 univalents) to his increase group, and the remaining 2 would be sterile combinations. The latter were, however, normal in habit. Our F_3 plants would all belong to the decrease group.

Owing to all these differences from expected results and from reported results in other crosses, it was thought that our 28 plants might not be representative—that they might have been an unconsciously selected group, possibly because of their greater health or of greater ease in counting their chromosomes. Evidence will be given later, however, which indicates that these plants were really a representative sample.

4. Genetic Results in F_2 and F_3 segregates.

(1) *The characters studied.*

Twenty pairs of characters were chosen for study. These were easily distinguishable in the parents. Some distinguish nearly all *dicoccum* from nearly all *vulgare* varieties, *e.g.* head form and compactness; others, such as the condition of the keel, are partially diagnostic; still others, such as the condition of the middle tooth of the glume, vary within both species. In Table IV the conditions of each of the twenty characters in

TABLE IV.

Character	*Dicoccum* parent	*Vulgare* parent
Stem thickness S	1·1–1·5 mm. at a point 2 cm. below head	1·6–2·2 mm.
Head form S	Ratio of 2-ranked side to 1-ranked side. ·613–·772	1·46–1·85
Compactness S	Average length of internode of head in mm. 3·1–4·0	4·2–5·1
Cavity of stem S	Stem solid at point 2 cm. below head	Hollow with thin walls
Collar	Structure like a collar at base of lowest spikelet extends all the way around stem	Extends part way around stem
Beards	Numerous. Longest 10–14 cm.	Few. Up to 2 cm.
Rachis segment S	Small, narrow at base and widening to twice its width at top	Broad, does not widen so much from base to top
Rachis hairs	None	Covered with short hairs
Rachis articulation S	Rachis easily disarticulated, each separate spikelet carrying with it the internodal portion immediately below it	Tough, spikelets come off leaving rachis intact
Glume adherence S	Glumes very hard to remove	Come off very readily
Glume shape	Empty glume long and narrow	Short and wide
Glume cross-section S	Prominent lateral nerve causes glume in an end view to appear like a flat-bottomed boat	Nerve absent. End view like a V with one arm longer than the other
Middle tooth	Very short	Longer
Lateral tooth	Close to base of middle tooth	Further away
Keel S	Fairly well developed throughout glume length	Exists only in upper half
Keel teeth	None	A number extending along half glume length
Seed shape S	Narrow, long, pointed	Short, plump
Seed cross-section S	Triangular with fairly distinct basal angles. Ventral surface flat. Narrow, shallow furrow	Rounded edges. Furrow deep and wide. Cheeks convex and plump
End of seed	Pericarp over embryo raised into longitudinal wrinkles terminating in point	Two rounded projections one below other. Surface smooth
Hairs on leaves	Long hairs on both sides	Few and short on one side. Scarcely any on other

the parental plants are briefly described. Where the conditions as recorded may be used to distinguish all or most *dicoccum* from *vulgare* varieties, the fact is indicated by the letter S in the first column immediately below the character designation.

(2) *Inheritance of individual characters.*

In 77 F_2 plants examined parental and intermediate conditions for most of the 20 characters were found. In the case of several characters,

particularly stem thickness, head form, and compactness, the range of variation in the segregates was beyond that of one or both parents. Where different heads of the same plant showed the two parental conditions of any character the plant was classified as intermediate for that character. Conditions not existing in either parent, for example, the middle tooth prolonged to a short awn, or a pointed lateral tooth, were found in a few segregates. The condition was classed as that which it resembled most.

Table V shows the results of classifying 77 F_2 plants as to each of nineteen characters. The *vulgare* condition is denoted by V, the *dicoccum* by D, intermediate by I, intermediate but more like *vulgare* by IV and intermediate but more like *dicoccum* by ID.

TABLE V.

Frequencies of various conditions of characters in 77 F_2 segregates.

		Class 1 characters						Class 2 characters												
Condition of character		Rachis articulation	Head form	Cavity	Compactness	Rachis segment	Seed cross section	Stem thickness	Glume adherence	Rachis hairs	Glume shape	Keel	Glume cross section	Seed shape	End of seed	Lateral tooth	Collar	Middle tooth	Keel teeth	Beards
F_1		D	I	I	V	V	I	V	I	V	I	D	I	I	I	V	I	V	V	IV
F_2	V	0	0	2	7	2	3	3	7	22	5	25	25	3	3	14	2	44	49	49
	IV	0	1	2	1	12	4	13	17	3	11	3	18	24	15	20	0	9	4	4
	I	2	11	13	4	11	26	13	23	7	34	8	13	30	18	28	52	10	15	11
	ID	4	10	14	2	35	34	4	8	21	20	4	13	17	35	3	2	6	7	5
	D	71	55	46	63	17	10	34	22	24	7	37	8	3	6	12	21	8	2	8
Totals V and IV		0	1	4	8	14	7	16	24	25	16	28	43	27	18	34	2	53	53	53
D and ID		75	65	60	65	52	44	38	30	45	27	41	21	20	41	15	23	14	9	13

The characters are divided into Classes 1 and 2. This division was made after the results had been tabulated, when it was seen that the great majority of the 77 plants had certain characters in the *dicoccum* or intermediate-*dicoccum* condition, and few or none showed *vulgare* or intermediate-*vulgare* conditions for these characters. Those characters in which the *dicoccum* condition characterised most of the plants were placed in Class 1, the others in which the various conditions were more evenly distributed were placed in Class 2. Generally speaking there was no question as to which class any one character belonged. Those characters in Class 2 which show the *vulgare* condition in only a few plants show the intermediate condition in many.

It will be observed that the characters in Class 1 are used to distinguish *dicoccum* varieties in general from *vulgare* varieties, while those in Class 2 cannot be so used or only to a limited extent. There are, however, exceptions. Glume-adherence, though falling in Class 2, is one of the best characters to use in distinguishing *T. dicoccum* from *T. vulgare*, but *T. spelta*, another 21-chromosome species, has the *dicoccum* condition. Stem thickness and keel can generally but not always be used. It is perhaps significant that of the characters in Class 2 these most closely approach Class 1 in genetic behaviour. The division into two classes is intended merely to call attention to the genetic facts, but it may throw light on what are taxonomically important characters. Most of the species-distinguishing characters (Class 1) are found in the *dicoccum* condition in all, or nearly all the segregates; the other characters (Class 2) are found in the *dicoccum*, *vulgare* or intermediate conditions with more evenly distributed frequencies.

That the very high proportion of segregates with *dicoccum* conditions of Class 1 characters is not due to Mendelian dominance is evident from the fact that in F_1 only one of these characters is in the *dicoccum* condition, two are *vulgare* and three intermediate (see first line of Table V). Certain Class 2 characters, notably the partially diagnostic ones, appear in the *dicoccum* condition in the majority of F_2, though F_1 are *vulgare*-like or intermediate. Other Class 2 characters are *vulgare*-like in F_1 and in the majority of F_2.

In nearly every case a satisfactory factorial interpretation of the genetic behaviour is impossible from the ratios obtained.

In *durum* × *vulgare* hybrids Thompson found quite different ratios, though many of the characters examined were the same as those used in this study. No classification of the characters into two groups was made. The *vulgare* condition of the individual specific characters was found in a much larger proportion of the F_2.

(3) *Correlation of characters and preponderance of* dicoccum-*like combinations.*

Since the individual species-distinguishing characters are found in the *dicoccum* condition in the great majority of F_2, most plants possess a combination of *dicoccum* characters. This is shown in Table VI for 28 individual plants of the 77 summarised in Table V. The 28 plants were those used in the cytological work. Table VI gives the condition of each of the 20 characters as well as the chromosome conditions in each of the 28 plants. The character called "hairs on leaves" was observed

TABLE VI.

Characters and chromosome numbers in F_1 and 28 F_2 segregates.

	Chromosome number			Class 1 characters								Class 2 characters															
Pedigree number	Metaphase plate	Bivalents	Univalents	Rachis articulation	Head form	Cavity	Compactness	Rachis segment	Seed cross section	Total V and IV	Total D and ID	Stem thickness	Glume adherence	Rachis hairs	Glume shape	Keel	Glume cross section	Seed shape	End of seed	Lateral tooth	Collar	Hairs on leaves	Middle tooth	Keel tooth	Beards	Total V and IV	Total D and ID
F_1	21	14	7	D	I	I	V	V	I	2	1	V	I	V	I	D	I	I	I	V	I	.	V	V	IV	6	1
F_2 80-6-14	14	14	0	ID	D	D	D	ID	V	1	5	V	V	D	I	V	IV	V	V	D	I	I	IV	V	V	9	2
80-6-30	14	14	0	ID	D	D	D	ID	I	0	5	D	IV	ID	ID	V	V	I	I	D	D	IV	V	V	V	7	5
80-1-12	14	14	0	D	D	D	D	ID	ID	0	6	D	D	ID	ID	D	I	I	IV	I	I	D	I	V	V	3	6
80-2-11	14	14	0	D	D	ID	D	ID	I	0	5	D	IV	D	I	IV	I	ID	ID	I	I	I	V	V	ID	4	5
80-3- 2	14	14	0	D	D	D	D	D	D	0	6	D	D	D	ID	D	IV	IV	ID	I	D	I	V	V	V	5	7
80-3-29	14	14	0	D	D	D	D	I	ID	0	5	D	ID	I	IV	D	D	IV	ID	IV	D	V	IV	V	I	6	6
80-5- 4	15	14	1	D	D	D	D	ID	ID	0	6	V	D	ID	I	D	IV	I	ID	IV	I	ID	D	ID	V	4	7
80-5-16	15	14	1	D	ID	D	D	D	ID	0	6	I	I	I	ID	V	IV	ID	IV	IV	I	ID	V	V	V	7	3
80-5-19	15	14	1	D	D	ID	D	D	I	0	5	D	D	I	I	V	I	D	I	IV	I	D	IV	V	V	5	4
80-5-21	15	14	1	D	D	D	D	ID	ID	0	6	I	D	ID	I	D	ID	ID	ID	ID	I	ID	I	ID	D	0	10
80-5-31	15	14	1	D	D	ID	ID	ID	IV	1	5	I	IV	V	I	ID	I	IV	ID	ID	I	I	V	V	I	5	3
80-6- 2	15	14	1	ID	D	ID	D	ID	IV	1	5	ID	IV	D	I	V	V	IV	V	I	D	D	V	V	V	8	4
80-2-25	15	14	1	D	D	ID	D	D	ID	0	6	I	D	I	ID	D	IV	ID	D	I	D	D	D	ID	ID	1	10
80-5-11	16	14	2	D	D	D	D	ID	IV	1	5	V	D	ID	IV	D	I	I	ID	IV	I	IV	I	I	V	5	4
80-5-25	16	14	2	D	D	D	D	I	I	0	4	V	IV	ID	IV	I	IV	IV	IV	IV	I	ID	IV	V	V	10	2
80-2- 9	16	14	2	ID	D	I	D	ID	IV	1	4	ID	IV	D	I	V	V	IV	ID	IV	D	D	I	I	V	6	5
80-3- 4	16	14	2	I	D	I	D	ID	ID	0	4	IV	IV	D	I	V	V	IV	IV	I	D	ID	V	ID	V	8	4
80-3- 9	16	14	2	D	D	D	D	ID	ID	0	6	D	I	ID	ID	I	IV	I	IV	D	D	IV	V	V	IV	6	5
80-5-10	17	14	3	D	D	D	D	ID	D	0	5	D	D	ID	ID	D	ID	D	ID	I	I	ID	D	V	V	2	10
80-5-26	17	14	3	D	D	D	D	D	I	0	5	I	I	D	I	V	I	ID	ID	I	I	I	V	V	V	4	3
80-2- 3	17	14	3	D	D	D	D	ID	ID	0	6	V	ID	ID	I	D	IV	I	IV	I	I	IV	V	V	D	6	4
80-2-10	17	14	3	D	I	ID	D	I	ID	0	4	I	D	V	IV	IV	V	IV	ID	V	ID	IV	V	V	I	9	3
80-5- 5	18	14	4	D	D	D	D	D	I	0	5	D	D	I	D	D	ID	ID	IV	D	D	V	V	V	V	5	8
80-6- 7	18	14	4	D	D	ID	V	ID	ID	1	5	D	D	IV	D	D	D	ID	ID	IV	D	I	V	V	I	4	8
80-3- 6	20 or 21	14 or 15	6	D	D	I	I	V	ID	1	3	ID	ID	V	IV	IV	V	I	D	V	I	I	ID	ID	I	5	5
80-2-20	19	15	4	D	IV	I	V	IV	ID	3	2	IV	I	V	I	V	IV	I	ID	V	I	IV	V	V	V	9	1
80-2-17	21	15	6	D	I	I	ID	IV	ID	1	3	IV	IV	V	I	V	IV	I	I	I	V	I	V	V	ID	8	1
80-1-19	20	17	3	D	I	I	V	IV	I	2	1	IV	IV	V	I	V	I	I	IV	V	I	I	V	I	I	7	0
Totals		V		0	0	0	3	1	1			5	1	6	0	11	6	1	2	4	1	2	16	20	16		
		IV		0	1	0	0	3	4			4	9	1	5	3	10	8	8	8	0	6	4	0	1		
		I		1	3	6	1	3	7			6	4	5	14	2	7	10	3	10	16	9	4	3	6		
		ID		2	1	7	1	15	14			3	4	9	7	1	3	7	13	2	1	6	1	5	3		
		D		25	23	15	23	6	2			10	10	7	2	11	2	2	2	4	10	5	3	0	2		

only in those plants used for cytological study, so that this character appears in Table VI but not in Table V. The characters are again divided into Classes 1 and 2, and the letters have the same meaning as before. At the right of each class are two columns showing the totals of the *vulgare*-like and *dicoccum*-like characters in that class for each plant. The plants are arranged in groups according to similarity of chromosome conditions.

It will be observed that 24 of the 28 plants showed the *dicoccum* or intermediate-*dicoccum* condition of almost all the six Class 1 (specific) characters. Only 2 of these 24 had the fully developed *vulgare* condition of a single one of the six characters. The remaining 4 plants showed a mixture of *dicoccum* and *vulgare* conditions or several intermediate conditions. Not a single plant was *vulgare*-like in the majority of these six characters. There is thus a strong correlation of the specific characters and a great preponderance of individuals with the *dicoccum* combination.

The Class 2 characters (most of which happen to distinguish the parental races used, but not all *dicoccum* races from *vulgare* ones) present a different situation. *Vulgare* conditions are much more numerous. Each plant shows a mixture of *vulgare* and *dicoccum* conditions of those characters though there is a tendency for one or the other to predominate in individuals. It is noteworthy that 3 of the 4 plants which are not *dicoccum*-like but intermediate in regard to the species-distinguishing characters, have few or no *dicoccum* characters of Class 2. There is a certain amount of correlation of Class 2 characters, but this is slight in comparison with that shown by those of Class 1.

In view of these results it was thought that the 28 plants used in the cytological work might have been an unconsciously selected group, and not representative of the whole population. In order to determine whether this was the case, 49 more plants were examined. These included all that grew in a section of the plot. (Table V, previously discussed, was made up from an examination of the whole 77.) It is not necessary to give the details for the individual plants, but the main results, so far as Class 1 characters are concerned, are summarised in Table VII. Group 1 means the 28 plants examined cytologically and recorded in detail in Table VI; Group 2 means the additional 49. It will be noticed that there is no significant difference between the two groups, the proportions having the various combinations being similar, except that Group 2 includes a somewhat larger proportion of intermediates. Nor did Class 2 characters show any significant difference in the two groups. It is clear, therefore, that the 28 plants used for cyto-

TABLE VII.

Comparison of frequencies of Class 1 *character combinations in the two groups.*

Combinations of Class I characters V D	Numbers of plants showing each combination Group 1	Group 2
0 – 6	8	16
0 – 5	7	16
0 – 4	3	2
0 – 3	0	1
0 – 2	0	1
1 – 5	5	2
1 – 4	1	1
1 – 3	2	1
2 – 4	0	1
2 – 3	0	2
2 – 2	0	5
2 – 1	1	1
3 – 2	1	0

logical study and reported in detail in Table VI are fairly representative of the F_2.

In Group 2 only 1 plant approached the *vulgare* type more closely than any in Group 1, and it had 13 *vulgare* characters, 3 intermediate and 3 *dicoccum*, 2 of which were important species-determining characters. No real *vulgare*-like segregate occurs in the whole 77. One plant had only 1 *dicoccum* character but it had 10 intermediate, and the *dicoccum* character was an easily disarticulating rachis, an outstanding character of the species[1].

In his study of *durum* × *vulgare* hybrids Thompson found a correlation of the *durum* characters on the one hand and of the *vulgare* ones on the other. The *vulgare* types were not so numerous. In our cross they are almost eliminated. No distinction was made into Class 1 and Class 2 characters though it was shown that certain *durum* ones were correlated more strongly than others. The plants which showed a mixture of *durum* and *vulgare* characters were more numerous than the corresponding ones in this *dicoccum* × *vulgare* cross.

The information available concerning F_3 for which chromosome counts were obtained, and concerning their F_2 parents, is given in Table VIII. The plan is the same as that of Table VI, and the plants are grouped in families. In regard to Class 1 characters there is an even stronger preponderance of *dicoccum* combinations than in F_2, not a single inter-

[1] Since this was written 133 more plants have been studied, making 210 in all. The results were similar to those just described. A single plant had all the species-distinguishing characters in the *vulgare* or intermediate-*vulgare* condition.

TABLE VIII.

Chromosomes and characters in 3 F_2 plants and 10 of their offspring.

		Chromosome number			Class 1 characters								Class 2 characters															
Generation	Pedigree number	Metaphase plate	Bivalents	Univalents	Rachis articulation	Head form	Cavity	Compactness	Rachis segment	Seed cross section	Total V and IV	Total D and ID	Stem thickness	Glume adherence	Rachis hairs	Glume shape	Keel	Glume cross section	Seed shape	End of seed	Lateral tooth	Collar	Hairs on leaves	Middle tooth	Keel teeth	Beards	Total V and IV	Total D and ID
F_2 parent	4–1–6				D	D	D	D	I	.	.	.	D	D	IV	D	D	D	.	.	IV	D	.	V	IV	I	.	.
F_3	4–1–6–2	17	14	3	D	D	D	D	ID	ID	0	6	I	D	I	I	ID	IV	I	I	I	I	D	V	ID	D	2	5
F_2 parent	4–2–4	.	.	.	D	ID	D	D	D	ID	.	.	D	ID	D	D	D	ID	ID	I	D	D	.	V	I	ID	.	.
F_3	4–2–4–2	15	14	1	D	ID	D	D	ID	D	0	6	I	ID	ID	ID	D	I	D	IV	D	D	I	V	V	D	3	8
	4–2–4–5	14	14	0	D	D	ID	D	ID	D	0	6	ID	D	ID	ID	D	D	D	IV	I	D	I	IV	I	ID	2	9
	4–2–4–6	15	14	1	D	D	D	D	ID	D	0	6	I	D	I	D	D	D	D	ID	I	D	D	ID	D	ID	0	11
	4–2–4–7	14	14	0	D	D	D	D	ID	D	0	6	ID	ID	ID	D	D	D	D	D	I	I	D	I	D	ID	0	11
F_2 parent	4–1–4	.	.	.	D	D	D	D	D	D	.	.	D	I	ID	D	D	D	I	D	I	D	.	D	I	V	.	.
F_3	4–1–4–1	15 (or 16)			D	D	D	D	D	D	0	6	D	ID	D	D	D	D	I	I	IV	D	I	I	I	D	2	8
	4–1–4–2	15	14	1	D	D	D	D	ID	D	0	6	D	D	I	D	D	D	ID	ID	IV	I	I	I	ID	I	1	8
	4–1–4–7	14	14	0	D	D	D	D	D	ID	0	6	D	D	ID	D	D	D	ID	ID	I	I	I	D	ID	ID	0	11
	4–1–4–8	15	14	1	D	D	D	D	ID	D	0	6	I	D	I	I	D	ID	D	ID	V	I	IV	I	D	V	3	6
	4–1–4–9	14	14	0	D	D	D	D	ID	ID	0	6	IV	I	D	ID	D	D	D	ID	I	I	V	D	I	V	3	7
	Totals in F_3 only	V and IV			0	0	0	0	0	0			1	0	0	0	0	1	0	2	3	0	2	3	1	2		
		I			0	0	0	0	0	0			4	1	4	2	0	1	2	2	6	6	5	4	3	1		
		D and ID			10	10	10	10	10	10			5	9	6	8	10	8	8	6	1	4	3	3	6	7		

mediate or *vulgare* condition appearing. The Class 2 characters also are found in the *dicoccum* condition much more frequently than in F_2. The number of families represented is too small to draw conclusions, and the F_2 parents are more *dicoccum*-like than the average. But as far as they go the results are in conformity with those of F_2. There is evident a strong tendency to return completely to the *dicoccum* condition. In several instances the *vulgare* condition in the F_2 is followed by *dicoccum* in F_3 whereas the reverse never occurred. Moreover, the intermediate condition in F_2 is followed by the *dicoccum* condition in F_3 much more frequently than by the *vulgare* condition.

5. Relationship between Cytological and Genetic Results.

The chromosome conditions and the characters of the segregates having been discussed, it is now possible to determine what relationship they bear to each other.

Table VI shows that 24 of the 28 F_2 had 14 bivalents and that the same 24 plants are to be classed as *dicoccum*-like on the basis of Class 1 characters. Four of the 28 segregates had more than 14 bivalents and the same 4 have been classed as intermediate. The plants in this latter group had 15 or 17 bivalents. Obviously there is a relationship between Class 1 characters which distinguish *dicoccum* varieties in general from *vulgare* and the number of bivalents—the closer that number approaches 14, the hapolid number of the *dicoccum* parent, the more *dicoccum* characters there are.

The possession of 1 to 4 univalents in addition to the 14 bivalents did not make the characters of the plant more *vulgare*-like than those of some which had no univalents. Judging from these results an extra bivalent is more effective than several univalents. The plant with 17 bivalents had the smallest number of *dicoccum* characters, and many intermediate.

In *vulgare* × *durum* F_2 segregates Sax and Thompson found, generally speaking, that 14- and 15-chromosome plants were *durum*-like, 20- and 21-chromosome plants were *vulgare*-like and the others were intermediate. No data on univalents and bivalents were available. When these results are compared with the ones just discussed it is seen that the relationship is quite different in the two cases. It is true that in *vulgare* × *dicoccum* F_2, 14- and 15-chromosome plants were found to be *dicoccum*-like for Class 1 and often for Class 2 characters, but 18 chromosome plants were equally *dicoccum*-like; 20- and 21-chromosome plants were not *vulgare*-like, and a 19-chromosome plant with more than 14 bivalents had more

vulgare characters than plants with 21 chromosomes. Moreover, there were no truly *vulgare*-like plants, a fact which is evidently related to the absence of the *vulgare* number of bivalents.

The correlation of chromosome conditions and characters as described for F_2 is borne out by the F_3 plants examined. All had 14 bivalents; all had *dicoccum*-like Class 1 characters. The Class 2 characters were more *dicoccum*-like than in F_2, and relatively few intermediate conditions were found. The plants were from three families with closely related chromosome numbers from 14 to 17 and they were all very like the *dicoccum* parent. The two families from which the majority of the plants were taken were relatively large, producing 9 and 10 mature plants respectively out of 16 seeds sown. It may be significant that the family from which the 17-chromosome segregate was secured had only 3 mature plants from 16 seeds.

6. REASON FOR PREPONDERANCE OF LOW CHROMOSOME NUMBERS AND *DICOCCUM* CHARACTERS.

In order to account for the missing expected types a number of possibilities were investigated.

(1) *Pollen sterility.*

The absence of expected types might be due to the abortion of pollen grains. Counts of bad pollen in F_1 flowers were therefore made. The pollen was mounted in lactic acid and fuchsin and observed immediately. The stained rounded grains were counted as good, the clear or shrunken as bad. The results were not very satisfactory. Considerable variation in the percentage of bad pollen was found in different stamens as shown by the following figures:

Dicoccum	1·81 to 7·24 %	bad pollen
Vulgare	1·06 „ 3·84	„
Dicoccum × *vulgare* F_1 ...	4·3 „ 15·3	„
Durum × *vulgare* F_1 ...	16·9 %	

The results differ from those of Hayes, Parker and Kurtzweil (2) who found all *dicoccum* pollen good and *vulgare* (Marquis) having less than 1 per cent. bad, and the average of reciprocal crosses between them having 6·45 per cent. bad pollen. It is clear however that there is a larger percentage of obviously poor pollen in these F_1 hybrids than in the parents, but the amount does not exceed 15 per cent. in *vulgare* ×

dicoccum. The one count of *durum* × *vulgare* shows a slightly higher percentage of obviously bad grains than the highest percentage found in *dicoccum* × *vulgare.*

(2) *Sterile flowers in* F_1.

It was thought that the absence of *vulgare* types might be due to non-development of seeds and this would be shown by sterile flowers. Accordingly several *vulgare* × *dicoccum* F_1 were examined and Table IX

TABLE IX.

Flower sterility in F_1 *and parents.*

	Sterile flowers in 74 spikelets								
	1st	2nd	3rd	4th	1st and 2nd	1st and 3rd	2nd and 3rd	1st, 2nd and 3rd	All 4th
Vulgare-dicoccum	19	26	47	71	5	10	16	3	2
Vulgare-durum	18	26	36	61	6	10	16	4	4
Vulgare	1	1	66	74	0	1	0	0	0
Dicoccum	3		74	74	0	—	—	—	—

shows the results secured from this examination and in addition similar results from *vulgare* × *durum* F_1 and *vulgare* and *dicoccum* pure lines grown on the same plot. Seventy-four spikelets of each were examined, after discarding those at the top and base of the ear, as they frequently fail to set seed in pure lines. In each spikelet the flowers which set seed were noted and the results tabulated. The first four columns show the numbers of spikelets in each case in which flowers 1, 2, 3 or 4 failed to set seed, regardless of whether any others did. The last four columns show the numbers of spikelets having different combinations of flowers in which seeds did not form. There is, therefore, a certain amount of duplication.

In pure *dicoccum* there were 3 spikelets in which only one seed was present, but they were brown and evidently diseased. It could not be ascertained whether the first or second flower was sterile. Only 2 flowers per spikelet ever set seed in *dicoccum*, and 3 was the maximum number in *vulgare*. That the hybrids occasionally set the fourth seed is doubtless due to increased vigour because of the hybrid condition or to the greater space each plant had while growing. The F_1 were grown a foot apart, the pure lines 4 inches.

It will be noted that the number of spikelets having a certain flower sterile increases with the distance that flower is from the base of the spikelet. This is to be expected as in pure lines the lower flowers are the ones which set seed.

Vulgare × *dicoccum* and *vulgare* × *durum* show great similarity in respect to sterility of flowers. The higher numbers of third and fourth sterile flowers in *vulgare* × *dicoccum* is probably accounted for by the difference between the *dicoccum* and *durum* parents since *dicoccum* sets only 2 seeds and *durum* often 3 per spikelet.

Table X shows the percentage of fertility on the basis of 1 to 4 flowers per spikelet. The hybrids and pure lines show a wide difference.

TABLE X.

Fertility in F_1 and parents.

	Percentage of fertility on basis of flowers per spikelet			
	1st flower	1st 2 flowers	1st 3 flowers	1st 4 flowers
Vulgare-dicoccum	74·33	71·62	59·46	45·27
Vulgare-durum	75·68	64·68	63·96	52·36
Vulgare	99·00	98·00	—	—
Dicoccum	97·00	96·50	—	—

In parental *vulgare* and *dicoccum* the spikelets from the middle of the ear practically always set seed in the first two flowers. That the first flower is the one to bear seed when only one is set was shown by an examination of numerous spikelets near the top and base of the ear. In no case was the contrary found to be true. With environmental conditions only affecting the setting of seed the first flower sets seed when any do. The conclusion is that over 20 per cent. of these *vulgare* × *dicoccum* flowers failed to set seed for some reason other than environmental factors. The *vulgare* × *durum* and *vulgare* × *dicoccum* were similar in this respect.

Fertility on the basis of two flowers per spikelet is the better method of comparison between hybrids and pure lines because of the difference between the parental *dicoccum* and *durum* lines in number of seeds set per spikelet, and also because of the different degrees of vigour accounted for above. The fact that the third flower does not set seed in *dicoccum* accounts for the fertility of *vulgare* × *dicoccum* segregates being greater than that of *vulgare* × *durum* on the two-flower basis and less on the three or four. The parental lines show 2 to 4 per cent. sterility in the first two flowers. After allowing for this 2 to 4 per cent. from ordinary causes there is about 25 per cent. of the first and second flowers in *vulgare* × *dicoccum* and over 30 per cent. in *vulgare* × *durum* F_1 plants which fail to set seed because of the hybrid condition.

(3) *Failure of F_2 to mature.*

If many seeds failed to germinate or to produce mature F_2 plants some of the missing types may be accounted for.

Table XI shows the number of seeds sown, the number and percentage of F_2 plants which have matured from these seeds, and similar data for some crosses between *vulgare* varieties. All the plants were grown within a few feet of each other in a very uniform piece of land.

TABLE XI.

Zygotic mortality in F_2.

	Seeds sown	Plants matured	Percentage
Vulgare-dicoccum	480	181	37·7
Vulgare-durum	960	604	62·9
Intra-*vulgare* crosses	1320	1120	84·8

A large proportion of F_2 plants failed to mature, but *vulgare* × *durum* seeds produced more plants than *vulgare* × *dicoccum*. It is probable that many of the seeds did not germinate, though observations were not made on this point. From a comparison of these data with those secured from intra-*vulgare* crosses it is obvious that about 50 per cent. of the *vulgare* × *dicoccum* and 25 per cent. of the *vulgare* × *durum* F_1 seeds failed to mature because of their hybrid condition.

(4) *Lost chromosomes.*

In a considerable proportion of the cases one or more lagging univalent chromosomes fail to reach the pole and to become incorporated in the daughter nuclei. They appear as darkly staining spots quite distinct from the reformed nucleus, and at later stages commonly become vacuolated. They eventually degenerate, and are lost. An attempt was made to determine the number of these lost chromosomes and the effect of the loss in reducing gametic numbers. Counts were made on several hundred microspore-tetrads mounted in iron-aceto-carmine. Various stages were studied from the conclusion of the homotypic division to the separation of the microspores. There was a very slight decrease in numbers during this period, owing to reabsorption by the nucleus or to degeneration, but the decrease was so slight that it may be disregarded. There is also a loss of chromosomes at the heterotypic division, but it is not necessary to record the counts made at that stage since the lost chromosomes are recaptured during homotypic division, or persist and are included in counts made at the tetrad stage.

Table XII gives the results obtained for both *dicoccum* × *vulgare* F_1 and for *durum* × *vulgare* F_1. In the *dicoccum* material 5 of the tetrads showed a supernumerary small cell in which lost chromosomes had become enclosed. In *durum* material no such extra cells were seen. It will

TABLE XII.

Frequency of lost chromosomes in vulgare × dicoccum *and* vulgare × durum.

Lost chromosomes	Number of cells		Proportion of cells	
	dicoccum hybrid	*durum hybrid*	*dicoccum hybrid*	*durum hybrid*
0	554	619	·518	·587
1	436	365	·409	·346
2	76	66	·083	·062
3	0	4	·000	·004
5th cell	5	0	—	—

be observed that about 50 per cent. of the cells showed lost chromosomes. If the 5 supernumerary cells contained only 2 lost chromosomes then in *dicoccum* × *vulgare* there was 1 lost chromosome for every 1·78 grains, while in *durum* × *vulgare* there was 1 for every 2·07 grains. If we assume that the loss is evenly distributed, that is, half of each kind of pollen grain is reduced to the kind with the next lower number, and that all resulting gametes function, the number of zygotes with chromosome numbers of 36 or more is less than one-quarter of the total. This is evidently an important factor in reducing the frequency of F_2 plants with the higher chromosome numbers. The table shows that *dicoccum* hybrids lose somewhat more than the *durum* ones. But this difference is probably not big enough to account for the difference between the two found in F_2 results.

7. DISCUSSION.

Kihara believes that all pollen is good and all gametes capable of functioning, but that the only zygotes which are capable of living normally are (1) those with 14 bivalents and 0–7 univalents, or (2) those with 21 bivalents and univalents combined, the extra 7 *vulgare* chromosomes all being represented at least once. The former he calls the "decrease" group, because in later generations they approach a stable 28-chromosome condition; the latter constitute the "increase" group because in later generations they approach a stable 42-chromosome condition. In addition there are rare "sterile combinations" which are dwarf, and set few seeds which germinate badly. These lack one or more *vulgare* chromosomes, having for example 20 bivalents, or 19 bivalents and 1 univalent.

Sax, on the other hand, believes that the sterility is gametic, and that this gametic sterility is responsible for the missing plants with the combinations of characters expected, and for the missing chromosome numbers. The nearer the chromosome number approaches either parental

condition the better the gamete functions. Those midway between the parental numbers do not function at all. The 14-chromosome segregates are *durum*-like and the 21-chromosome segregates are *vulgare*-like because the *vulgare* factors are carried in the extra 7 *vulgare* chromosomes while the other 14, which mate with *durum* chromosomes, are essentially similar to them. A 14-chromosome plant is then *durum*-like even if all its chromosomes come from the *vulgare* parent.

It is clear that the amount of gametic sterility which reveals itself as visibly bad pollen is much too small to account for the results. Not more than 15 per cent. of the pollen is bad. Watkins (10) reports, however, that the apparently good pollen may not be capable of functioning. This conclusion was reached from a study of the germination of the pollen on the stigmas. He found a high percentage of apparently good pollen grains remaining ungerminated and believes that these grains are the ones with the intermediate chromosome numbers. All the female gametes, on the other hand, he believes to be fully capable of functioning. His experimental results agree with the supposition that only 14- and 21-chromosome male gametes function.

It is evident from Table I that in 22 of the 28 cases in our *dicoccum* hybrids, one or both gametes which joined must have had more than 14 and fewer than 21 chrosmosomes. At least 13 of the 56 gametes had only 14. The majority must have had only 1 or 2 more than 14.

That there is a good deal of the zygotic sterility which Kihara considers to be the important factor is evident from the fact that 50 per cent. more seeds fail to grow into mature F_2 plants than in the parental races. Even this is not enough, however, to account for the results as may be seen by referring to Table II. It is possible that to this should be added the 25 per cent. sterility of F_1 flowers, since the embryos may form but fail to develop. This sterility may also be due, however, to failure of gametes to function. On the whole it seems that zygotic sterility, which is evident and extensive, is not sufficient to account for the results, and must be supplemented by hidden gametic sterility, selective fertilisation or some other factor. The total amount of sterility in our cross is made up as follows: about 15 per cent. of the pollen is obviously bad; 25 per cent. of F_1 flowers in positions in which seed is set in pure races are sterile; 50 per cent. more seed fail to produce mature plants in the hybrids than in pure lines.

In regard to the correlation of characters and chromosome numbers, Thompson has pointed out that certain facts do not fit the theory that all the *vulgare* characters are carried in the extra 7 *vulgare* chromosomes

and that the other 14 carry only *durum* characters so that a 28-chromosome plant is *durum*-like even if most of its chromosomes come from the *vulgare* parent. Some of these facts are: (1) Some well-known *durum* varieties have one or few *vulgare* characters and *vice versa*. (2) Some 28-chromosome segregates have one or few *vulgare* features, even the most characteristic. (3) Some characters are present in 14-chromosome wheats, absent in those with 28, and present again in those with 42. (4) Certain characters which *vulgare* possesses and *durum* lacks are present in other 28-chromosome wheats. It was therefore suggested that factors determining or influencing *vulgare* characters were present in many or all the chromosomes, not merely in the extra 7, and that sterility, observed chromosome numbers, and correlation of characters might be due to chromosome incompatibilities. Only certain combinations of chromosomes, chiefly *durum* or chiefly *vulgare*, would work together. In addition to the facts mentioned above this suggestion would account for the existence of partially sterile 28-chromosome plants, and the failure of the seeds to produce mature offspring.

From Table VI it will be seen that our 6 plants with 28 chromosomes had 1 *vulgare* character, 3 intermediate, and several intermediate-*dicoccum* in Class 1 (species-distinguishing characters). The absence of the extra 7 *vulgare* chromosomes is associated, therefore, with the nearly but not quite complete absence of *vulgare* characters. If there are no chromosome incompatibilities and all combinations of the 28 chromosomes are viable, the extra 7 *vulgare* ones must be chiefly but not entirely responsible for the *vulgare* characters. Characters which distinguish most *dicoccum* forms from *vulgare*, such as the nature of the keel and the thickness of the stem, are seen frequently to be in the *vulgare* condition in these 28-chromosome plants and cannot, therefore, be determined by the 7 *vulgare* chromosomes. The loose adherence of the glumes which distinguishes *vulgare* proper from all *dicoccum* forms is present in half the 28-chromosome segregates. But *T. spelta* which also has 42 chromosomes shows the tight adherence of *dicoccum*.

The table also shows that the addition of 3 or 4 of the 7 *vulgare* chromosomes to the 28 does not necessarily add any more *vulgare* characters, since the 32-chromosome plants are quite as *dicoccum*-like as those with 28, in regard to both Class 1 and Class 2 characters. But the presence of two homologous chromosomes which are able to form a bivalent does produce some effect. The plants with 15 bivalents are somewhat intermediate. They all have a number of univalents as well, but the same number of univalents without bivalents produces no effect.

The Class 2 characters, which for the most part cannot be used to distinguish the two species, are affected at least as much as those of Class 1 by the presence of extra *vulgare* chromosomes, as may be seen by reference to the last four plants in Table VI. One may conclude that even if the suggested factor of chromosome incompatibilities be left on one side and all combinations of the 14 primary chromosomes be considered viable, the extra 7 *vulgare* chromosomes cannot be completely responsible for *vulgare* characters, that the 14 primary ones must play some part in their determination, and also that the extra 7 are concerned in part with the characteristics which vary within both species.

Another problem presented by our results is the deficiency of *vulgare*-like character combinations and chromosome numbers. Sax and Thompson have found in *durum* × *vulgare* a smaller number of 42- than of 28-chromosome segregates. In our cross only 3 plants had more than 34, 2 of these had 36, and the third had 37. Eighteen of the 28 plants had 30 chromosomes or fewer. Similarly, very few segregates were of the *vulgare* type in most of the species-distinguishing characters. It appears that some factor which tends to inhibit the development of *vulgare*-like segregates with higher chromosome numbers has been much more effective in this case.

That this factor is not gametic sterility which can be detected visibly is evident from a comparison of the percentages of bad pollen in *dicoccum* × *vulgare* and *durum* × *vulgare* hybrids. It may be due to the *dicoccum* hybrids having a larger percentage of apparently good but really deficient pollen. Watkins reports much pollen of this kind in *turgidum* × *vulgare* hybrids and believes that the failure of flowers to set seed is due to a lack of good pollen. But as *dicoccum* hybrids had as high a percentage of fertile flowers as *durum* or *turgidum* hybrids this cannot account for the peculiar results with *dicoccum* hybrids. It is possible that there may be a greater proportion of really bad pollen in *dicoccum* hybrids and still enough left to cause as frequent fertilisation as in *durum* hybrids. If so the extra bad pollen in *dicoccum* hybrids must have had the higher chromosome numbers.

The approximately equal fertility of *dicoccum* × *vulgare* and *durum* × *vulgare* flowers, shows that the results cannot be due to greater mortality of young *dicoccum* zygotes.

The mortality of the zygotes at a later stage—after seed formation—may be an important factor; 25 per cent. more seeds of *durum* × *vulgare* than of *dicoccum* × *vulgare* developed into mature F_2 plants under the same conditions. This 25 per cent. may represent missing plants with

higher chromosome numbers. It is of interest in this connection that in a cross between another variety of *dicoccum*, namely Khapli, and *vulgare* we found almost complete zygotic mortality. More than 80 crossed seeds were planted, many failed to germinate, and all but two of the seedlings died before reaching a height of 8 inches. Only those two ever formed heads.

The loss of univalent chromosomes through failure to become incorporated in the daughter nuclei, is an important factor in reducing the frequencies of the higher chromosome numbers. But this will probably not account for the differences between the F_2 results since *dicoccum* hybrids lost only a few more than *durum* hybrids.

There is the further consideration that *T. dicoccum* is less closely related to *T. vulgare* than is *T. durum* or *T. turgidum*. It is possible therefore that chromosome incompatibilities are greater—that it is more difficult to secure workable combinations of *dicoccum* and *vulgare* chromosomes. In some *dicoccum* × *vulgare* crosses this clearly seems to be the case. Even the F_1 of Khapli × *vulgare* can rarely be brought through to maturity, nearly all plants dying at an early stage. In this case much of the mortality is certainly zygotic but in other crosses in which F_1 develops normally it may also be gametic. It is to be expected that incompatibilities would be greatest where the extra *vulgare* chromosomes are most numerous.

Whatever interpretation is placed on the results reported, they show that segregates with most of their important distinguishing characters in the *vulgare* condition are very rarely secured in a *dicoccum* × *vulgare* cross. It will therefore be very difficult to combine by breeding operations any desirable characters of *dicoccum* with those of *vulgare*. Even if segregates which are of the general *vulgare* type are secured, there will be the further great problem of detaching the particular *dicoccum* character desired. Breeders who use *dicoccum* as one parent must expect very different results from those of other species-crosses in wheat and must be prepared to raise very large second and later generations.

8. SUMMARY.

In crosses between 14- and 21-chromosome wheats the F_2 show chromosome numbers and combinations of characters which approach those of the parents much more closely than is to be expected if all gametes are functional and all zygotes viable. In results hitherto reported the conditions of the 21-chromosome parent were represented nearly as frequently as those of the parent with 14 chromosomes.

A cytological examination was made of 28 F_2 hybrids between *T. dicoccum* (14) and *T. vulgare* (21). Twenty-four plants had 14 bivalent chromosomes and 0–4 univalents; only 1 had as many as 17 bivalents; only 3 plants had more than 34 single chromosomes, and the greatest number was 37. The great preponderance of low numbers approaching that of the *dicoccum* parent and the absence of those approaching the *vulgare* number, are evident. F_3 results were similar.

Twenty pairs of characters which distinguish the parents were studied in these 28 and in 49 (later, 182) additional F_2. On the basis of genetic behaviour the characters fall into two classes: (1) those found in the *dicoccum* condition in all or nearly all the segregates, (2) those found frequently in the *vulgare* or intermediate as well as in the *dicoccum* condition. The characters in Class 1 prove to be those which most generally distinguish *dicoccum* varieties taxonomically from *vulgare* varieties. Most of those in Class 2 are not of general taxonomic value but happen to distinguish the varieties used in this investigation. The great majority of individual plants were *dicoccum*-like in species-distinguishing characters; the remainder were intermediate.

The numerous *dicoccum*-like plants were those which had 14 bivalent chromosomes; the few intermediate plants were those with 15–17 bivalents. *Vulgare*-like combinations of characters and chromosome numbers are very rare. The presence of 1–4 univalents in addition to the 14 bivalents has no effect in making the characters *vulgare*-like or intermediate. The presence of additional bivalents has some effect in this respect.

The primary 14 as well as the extra 7 *vulgare* chromosomes are concerned to some extent in the determination of *vulgare*-characters. The extra 7 are also concerned to some extent in determining non-specific characters.

Several possibilities were investigated to account for the missing expected types.

(1) The proportion of visibly bad pollen is insufficient to account for the difference between actual and expected results or for the difference between *dicoccum* × *vulgare* and other hybrids.

(2) Twenty-five per cent. of F_1 flowers in a favourable position for setting seed failed to do so. These may represent missing types, but cannot account for the differences between this and other crosses between 14- and 21-chromosome species for *durum* × *vulgare* F_1 showed as great sterility.

(3) Fifty per cent. more F_2 seed failed to produce mature offspring

than is the case in pure races, whereas in the *durum* × *vulgare* cross the percentage was only 25.

(4) About 50 per cent. of young F_1 pollen grains show lost chromosomes. This would probably reduce the number of F_2 zygotes with 36 or more chromosomes to less than one-quarter of the whole. Though *dicoccum* × *vulgare* hybrids show a somewhat greater loss than *durum* × *vulgare* the difference is not sufficient to account for the results.

(5) The taxonomic differences between *dicoccum* and *vulgare* are greater than between other 14-chromosome wheats and *vulgare*, and may indicate greater chromosome incompatibilities.

The difficulty of combining, through breeding operations, desirable qualities of *dicoccum* with those of *vulgare* will be very great because of the correlation of *dicoccum* characters, and particularly because of the rarity of *vulgare*-like segregates.

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DISCONTINUOUS VARIATION AND HETEROGONY IN *FORFICULA*[1]

BY J. S. HUXLEY.

(With Six Text-figures.)

SINCE Bateson and Brindley (1892) showed that the forceps of *Forficula* and the "horns" of the beetle *Xylotrupes* showed a bimodal frequency curve, while that for body-size was unimodal, little further advance has been made with the problem. Since the organs in question both appeared to be heterogonic, and since I had succeeded in showing for another heterogonic organ a quantitative law of growth (Huxley, 1924) it seemed that it would be profitable to investigate the matter along these lines. Just about this time the interesting paper by Djakonov (1925) appeared, in which he gave evidence indicating that the dimorphism of the earwig's forceps was probably not genetic. Neither this paper, however, nor that of Bateson and Brindley gave tables of measurements of body-length and organ-length, individual by individual. In passing, I should like here to enter a plea for making it an invariable practice of giving in full such data as constitute the raw material of the evidence for any results obtained: it is often impossible to know in advance what purposes the facts may be made to serve, and failure to do so may mean that some other investigator has to make over again a whole series of laborious measurements. In this case, the data luckily survived. I have to acknowledge, with many thanks, the kindness of Mr Brindley in turning over to me his *Xylotrupes* measurements, and to Prof. J. Philiptschenko for doing the same with those on *Forficula* made by Dr Djakonov, after the latter's untimely death.

In both cases I have arranged the material in the form of a correlation table—a simple procedure which enabled certain interesting facts to be readily made out. In this paper I shall deal only with the data for *Forficula*.

Forficula auricularia.

Djakonov's measurements were made usually to 0·5 mm. When a magnitude was exactly on the 0·25 or 0·75 mm. mark, it appears to have been entered as such. I soon decided, however, that with regard to the forceps-length it was for my purpose quite unnecessary to go beyond 0·5 mm., and with regard to the body-length beyond 1 mm. classes.

[1] *Studies in Heterogonic Growth*, No. 3.

The ultilisation of the full detail of the measurements would have involved a good deal more labour, and would in places have obscured the broad outline of the results. Besides, it is quite clear to my mind that any further step towards the solution of the problems involved must come by way of experiment; measurements and their analysis can only here show us how to direct our experimental procedure. As it is, some facts emerge perfectly clearly.

The results are all set down in Table I. Five lots of measurements have been tabulated separately, and also their sum. Group *A* comprised 445 individuals[1] collected in 1918; Group *E*, 92 collected in 1922. Groups *B*, *C*, *D* were all collected in 1921; the two former were from their normal habitat under the bark of tree-stumps, the last one from a tree-stump which had had the bark deliberately stripped from it shortly before; the earwigs had not left the stump, but had continued to live on there, changing their habits so as to burrow into the wood-fibre. The resulting conditions, as Djakonov shows, were in all probability less favourable than those of the normal habitat. Group *B* differs from *C* in that it was collected early in the season, when many insects had only just moulted into the imaginal condition. As a result, the body-length averages less than normal (see Djakonov, p. 223).

The facts which emerge from the table may be summarised as follows:

(1) In most (but not all) body-size classes, the characteristic bimodality of forceps-length seen in the collections as wholes is still very evident. In every case, it is seen for the 13, 14, and 15 mm. body-length classes; in the collected figures for the five groups together, it is also apparent in those of 11, 12, and 16 mm.

(2) However, in every table there are some body-length classes which do not show this bimodality, but are *unimodal* for forceps-length. When this is so, the mode shown always clearly coincides with one or the other of the two modes of the bimodal classes. For small-bodied animals, it is the low mode ("form brachylabia"); for large-bodied, the high mode ("form macrolabia"). The 10 and 17 mm. body-length

[1] I have taken the data direct from Djakonov's MS. tables. In his paper, in the curves for forceps-length he includes individuals whose bodies were not measurable, and *vice versa*, hence my numbers are always smaller than his. I have divided his Group 1921 *a* (see his text) into two groups for reasons given by him. His data for 1920 were not available to me. He himself points out that body-length is not the most accurate measure of size, owing to shrinkage, etc. However his data show strong correlation of body-length and pronotum-breadth; and, since the body-length measurements are the most abundant, I have chosen them. I am convinced that the errors involved are not large, when the averages of large samples are concerned.

TABLE I.

(Modal values are printed in heavy type.)

Group	Class by body-length mm.	No. in Class	Mean body-length mm.	Mean forceps-length mm.	Forceps-length mm. 3·5	4·0	4·5	5·0	5·5	6·0	6·5	7·0	7·5	8·0	8·5	9·0	9·5	10	b-series Total number	b-series Mean forceps-length mm.	b-series Relative forceps-length %	m-series Total number	m-series Mean forceps-length mm.	m-series Relative forceps-length %	% m-type in class
A (1918, 1 & 1a)	10	4	—	—	**2**	**2**	—	—	—	—	—	—	—	—	—	—	—	—	4	3·75	37·5	—	—	—	0·0
	11	8	—	—	1	**6**	—	1	—	—	—	—	—	—	—	—	—	—	8	4·06	36·9	—	—	—	0·0
	12	52	—	—	6	**20**	10	5	1	2	1	2	4	—	1	—	—	—	43	4·24	35·3	9	7·22	60·2	17·3
	13	127	—	—	3	**21**	12	11	5	9	14	**23**	20	6	3	—	—	—	**50**	4·40	33·8	77	7·00	53·8	60·6
	14	142	—	—	1	**12**	**12**	6	3	10	20	20	**27**	19	11	1	—	—	33	4·41	31·5	**109**	7·24	51·7	76·8
	15	91	—	—	—	**2**	**2**	1	1	4	9	14	**24**	17	11	5	1	—	5	4·50	30·0	86	7·56	50·4	94·5
	16	19	—	—	—	—	**1**	**1**	—	—	—	4	2	**7**	4	—	—	—	2	4·75	29·7	17	7·79	48·7	89·5
	17	2	—	—	—	—	—	—	—	—	—	—	—	—	**1**	—	—	1	—	—	—	2	9·00	52·9	100·0
	Total	445	13·7	6·33	13	63	37	25	10	25	44	63	77	49	31	6	1	1	145	4·32	—	300	7·30	—	67·4
B (1921, a. 1)	10	1	—	—	**1**	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3·50	35·0	—	—	—	0·0
	11	13	—	—	2	**7**	1	2	—	**1**	—	—	—	—	—	—	—	—	**12**	4·13	37·5	1	6·00	54·5	7·7
	12	21	—	—	3	**6**	3	—	2	**2**	1	2	1	1	—	—	—	—	**12**	4·00	33·3	9	6·56	54·7	42·9
	13	29	—	—	2	**9**	1	—	1	2	1	**6**	1	6	—	—	—	—	**12**	3·96	30·5	**17**	7·18	55·2	58·6
	14	17	—	—	—	**1**	**1**	—	2	1	**3**	2	2	2	**3**	—	—	—	2	4·25	28·3	15	7·13	47·5	88·2
	15	2	—	—	—	—	—	—	—	—	**1**	**1**	—	—	—	—	—	—	—	—	—	2	6·75	45·0	100·0
	16	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**1**	—	—	—	—	1	9·50	59·4	100·0
	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Total	84	12·7	5·64	8	23	6	2	5	6	6	11	4	9	3	—	1	—	39	4·03	—	45	7·04	—	53·6
C (1921, a. 2–4)	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	11	1	—	4·00	—	**1**	—	—	—	—	—	—	—	—	—	—	—	—	1	4·00	36·4	—	—	—	0·0
	12	19	—	3·92	3	**16**	—	—	—	—	—	—	—	—	—	—	—	—	19	3·92	32·7	—	—	—	0·0
	13	95	—	4·51	5	**56**	12	4	3	**6**	**6**	1	1	1	—	—	—	—	78	4·10	31·5	17	6·38	49·1	17·9
	14	174	—	5·70	6	**73**	20	10	7	11	11	**21**	10	4	1	—	—	—	**112**	4·19	29·9	62	6·81	48·6	35·6
	15	161	—	6·20	2	**25**	15	7	7	13	10	**33**	**33**	14	2	—	—	—	50	4·30	28·7	**141**	7·06	47·1	68·9
	16	94	—	7·17	—	1	**5**	3	4	2	6	13	**30**	23	7	—	—	—	12	4·83	30·1	82	7·50	47·0	87·2
	17	13	—	8·00	—	—	—	—	—	1	—	1	1	4	**5**	1	—	—	—	—	—	13	8·00	47·1	100·0
	Total	557	14·45	5·69	16	172	52	24	21	33	33	69	75	46	15	1	—	—	272	4·19	—	285	7·14	—	51·1

TABLE I (*continued*).

Group	Class by body-length mm.	No. in Class	Mean body-length mm.	Mean forceps-length mm.	Forceps-length mm. 3·5	4·0	4·5	5·0	5·5	6·0	6·5	7·0	7·5	8·0	8·5	9·0	9·5	10	*b*-series Total number	*b*-series Mean forceps-length mm.	*b*-series Relative forceps-length %	*m*-series Total number	*m*-series Mean forceps-length mm.	*m*-series Relative forceps-length %	% *m*-type in class
D (1921, b)	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	11	9	—	4·00	3	6	—	—	—	—	—	—	—	—	—	—	—	—	9	3·83	34·8	—	—	—	0·0
	12	52	—	3·92	10	40	2	—	—	—	—	—	—	—	—	—	—	—	52	3·92	32·7	—	—	—	0·0
	13	88	—	4·51	3	40	15	3	4	6	7	4	6	—	—	—	—	—	61	4·15	31·9	27	6·54	50·3	30·7
	14	124	—	5·70	4	27	23	4	4	8	12	18	13	9	1	1	—	—	60	4·28	30·6	64	7·03	50·2	51·6
	15	56	—	6·20	—	4	4	1	1	4	5	7	16	11	3	—	—	—	9	4·33	28·9	47	7·33	48·9	83·9
	16	12	—	7·17	—	—	—	—	—	—	1	1	2	5	2	1	—	—	—	—	—	12	7·88	49·3	100·0
	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Total	341	13·6	5·43	20	117	44	8	9	18	25	30	37	25	6	2	—	—	191	4·12	—	150	7·10	—	44·0
E (1922)	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	11	9	—	—	—	6	2	—	—	—	1	—	—	—	—	—	—	—	8	4·13	37·5	1	6·50	59·1	11·1
	12	16	—	—	1	9	1	1	2	—	1	1	—	—	—	—	—	—	13	4·19	34·9	3	6·33	52·8	18·75
	13	24	—	—	1	11	6	—	—	—	2	3	1	—	—	—	—	—	18	4·14	31·8	6	6·92	53·2	25·0
	14	24	—	—	—	4	3	1	3	—	4	4	5	—	—	—	—	—	9	4·44	31·7	15	6·83	48·8	62·5
	15	16	—	—	—	3	—	2	1	2	2	1	4	1	—	—	—	—	5	4·50	30·0	11	6·86	45·8	68·7
	16	3	—	—	—	1	—	—	—	—	—	—	1	1	—	—	—	—	1	4·00	25·0	2	7·75	48·4	66·7
	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Total	92	13·3	5·32	2	34	12	4	6	2	10	9	11	2	—	—	—	—	54	4·19	—	38	6·86	—	41·3
Totals, *A–E*	10	5	—	3·70	3	2	—	—	—	—	—	—	—	—	—	—	—	—	5	3·70	37·0	—	—	—	0·0
	11	40	—	4·15	6	26	3	3	—	1	1	—	—	—	—	—	—	—	38	4·04	36·7	2	6·25	56·8	5·0
	12	160	—	4·41	23	91	16	6	5	4	3	5	5	1	1	—	—	—	139	4·05	33·8	21	6·81	56·8	13·1
	13	363	—	5·24	14	137	46	18	13	23	30	37	29	13	3	—	—	—	219	4·18	32·2	144	6·86	52·8	39·7
	14	481	—	5·80	11	117	59	21	19	30	50	65	57	34	16	2	—	—	216	4·26	30·4	265	7·06	50·4	55·1
	15	326	—	6·61	2	34	21	11	10	23	27	56	77	43	16	5	1	—	69	4·32	28·8	257	7·23	48·2	78·8
	16	129	—	7·28	—	2	6	4	4	2	7	18	35	36	13	1	1	—	15	4·77	29·9	114	7·61	47·6	88·4
	17	15	—	8·17	—	—	—	—	—	1	—	1	1	4	6	1	—	1	—	—	—	15	8·17	48·1	100·0
	Total	1519	13·87	5·80	59	409	151	63	51	84	118	182	204	131	55	9	2	1	701	4·19	—	818	7·17	—	53·9
Range as % of mean			12·6	17·4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6·9	—	—	6·1	—	48·4

classes are unimodal throughout, and in addition the 11, 12, and 16 mm. classes are unimodal in one or more of the separate groups.

(3) There is a very obvious correlation between body-length and forceps-length, as seen in the trend of the figures in the correlation tables (Fig. 5). Djakonov has in two instances computed the correlation coefficient (pp. 211, 213), and found it to be about 0·6. However, in view of the complication introduced by the bimodality, this figure does not tell us very much in detail. A perhaps better method was also practised by him, viz. taking the mean size of body for all the *brachylabia* forms (*i.e.* all those which are grouped round the low mode) and also for the *macrolabia* forms[1]. When he did this he found, *e.g.* with Group *A*, that the one had a mean body-length of 12·96, the other one of 14·43 mm.

The facts given under (2) above bring this out in yet another way. When the size of body falls below a certain length, *no* macrolabia forms are produced, and conversely, *no* brachylabia when the size of the body rises above a certain limit.

(4) For brevity's sake, let us speak of the brachylabia forms grouped around the low mode as the "low" or *b*-series, the macrolabia forms as the "high" or *m*-series. If we now, for each body-length class, take the mean forceps-length, we obtain the results given on the right of the table. We find that with increasing length of body there is an increasing mean length of forceps, in both *b*- and *m*-series. This relation is on the whole remarkably regular. When there are irregularities, they are invariably associated with small numbers in the particular class and are thus presumably mere errors of random sampling. For the totals, the mean of the *b*-series rises with body-length from 3·70 to 4·77 mm., that of the *m*-series from 6·25 to 8·17 mm. Very similar figures are found in the separate groups[2].

[1] As will be seen from the tables, the two classes often slightly overlap. This can be overcome in two ways. Djakonov cuts the knot by taking an arbitrary standard, and counting all individuals with forceps up to a length of 5 mm. inclusive as *brachylabia*, all those with larger forceps as *macrolabia*. I have preferred, since it seemed to me that there was no reason for supposing that the point of division of the two classes might not shift with conditions, environmental or genetic, to examine each body-length class separately and to split it up into the two types "on its merits"; when there is an overlap, the members of the minimum class have been distributed to the two sides according to what seemed probable from simple inspection. In many cases (*e.g.* Group *A* versus Group *B*) this procedure undoubtedly is an improvement. And the errors introduced by arbitrary assignment of the overlap class are not significant.

[2] It may be mentioned here that Brindley (1914 *a* and *b*) has recorded numerous earwigs with forceps-length over 10 mm., the maximum observed being 12·25 mm. Rough measurement of Brindley's figure of this specimen indicates that its body-length was over 19 mm.

(5) This, it will be said, is what would naturally be expected. If, however, instead of the absolute mean forceps-length, we take the *relative* mean forceps-length, expressed as percentage of body-length, we obtain a result which, to me at least, was wholly unexpected. Within each series, the relative forceps-length *diminishes* instead of increasing with increasing body-length. Taking the totals again, we see that the relative forceps-length in the *b*-series decreases from 37·0 to 29·9 as the body-length increases from 10 to 16 mm., that of the *m*-series decreases from 56·8 to 48·1 as the body-length increases from 11 to 17 mm. In other words, we have a phenomenon which is essentially the reverse of that seen in *Xylotrupes* (Huxley, in press). In the beetle, within either series the horns increase relatively faster than the body; in the earwig, the forceps within either series increase relatively slower than the body.

What bearing have these facts upon Djakonov's thesis, viz. that the bimodality is neither a genetic phenomenon in its origin, nor dependent upon selective mortality, but is the expression of some developmental law? He believes that the two modes represent positions of relative equilibrium as regards absolute forceps-length. He adduces as a parallel example De Vries' (1901) fasciated strain of *Dipsacus*, which always threw a percentage of plants with fasciated stems. However, it also threw a percentage of normals, and although the two types could, by environmental agencies, be made to appear in very different proportions, no intermediates ever occurred. The state of affairs in *Forficula* could not be expected to be so clear-cut, since the two equilibrium-positions differ only quantitatively, not qualitatively; however, from his figures and those of Bateson and Brindley it is clear that the overlap of the *b*- and *m*-series is very slight, and this in spite of the proved unimodality and typical form of the curve for body-size, as measured not only by length, but by pronotum-breadth and other values.

The further facts on which he relies to prove his thesis are briefly as follows:

(1) When, for the group here called *D*, he artificially created a less favourable environment than that of *C*, by stripping off the bark which formed its natural habitat, the mean body-length was slightly decreased, and the percentage of *brachylabia* distinctly increased.

(2) When individuals regenerate one member of the paired forcipes after natural or experimentally-induced loss not too long before the last moult[1], the other, *intact* member of the pair is always of the *b*-type,

[1] Male and female earwigs resemble each other as regards their forcipes until their last moult. Before this the forcipes are small, and unimodal in frequency in both sexes. The fact is of considerable interest from the standpoint of developmental physiology.

never more than 5·5 mm. long. This fact is to be explained by the rapid growth of the regenerate exerting an abnormal drain upon the food-supply available for the development of the pair of forcipes.

(3) Infection with the larva of the fly *Digonichaeta setipennis* is common (found in about 15 per cent. of dissected adults). Of 46 infected specimens dissected, only one of *m*-type was found. The rest were all of the *b*-type, although the uninfected specimens showed the two types in nearly equal proportions. Infection also induces a slight reduction of the general body-size.

(4) Of the comparatively few specimens bred in the laboratory, *all* were of *b*-type, although a majority of the fathers were *m*-type. This makes it probable that the two types are not *per se* inheritable, and that the unfavourable conditions of the laboratory prevent the appearance of *m*-type specimens. (It must be admitted, of course, failing more extended breeding tests, that Djakonov has not eliminated the possibility that the *b*-type is dominant, although this alternative is unlikely.)

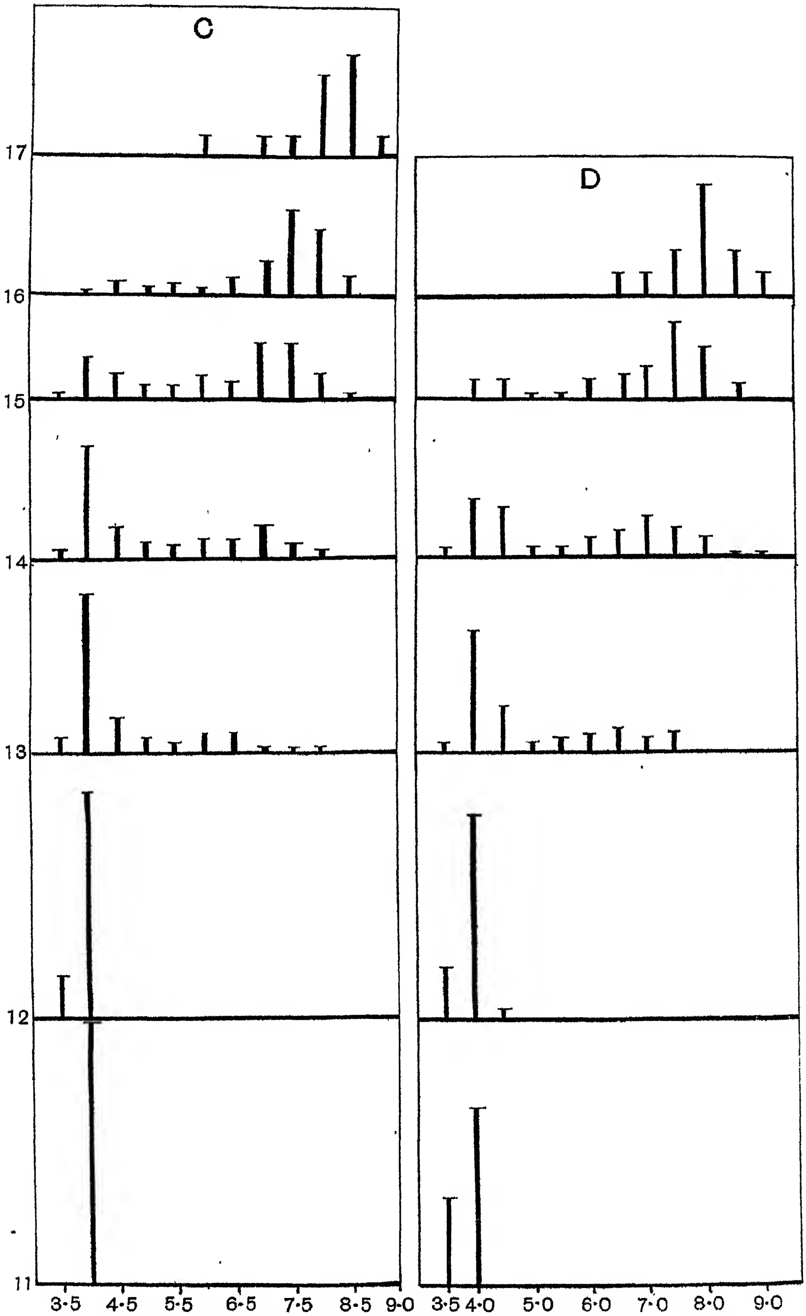
Djakonov thus concludes that the *b*- and *m*-types represent simply two "reaction-norms" of one genetic constitution, and that favourable conditions induce the large, unfavourable conditions the small type of forcipes. Bateson and Brindley hinted at this when they wrote (*l.c.* p. 589) "this will be recognized as an instance of Variation about two positions of stability, the intermediate position being one of less stability."

Now further analysis of the tables as constructed on a correlation basis from Djakonov's data shows some facts relevant to this point.

Instead of considering the *b*- and *m*- series separately, we may lump them together and take the means for the whole number of individuals of each body-length. The results are given in Table I, column 5. When the means thus obtained are plotted against body-length, logarithmically both ways, a close approximation to a straight line, with an angle of $> 45°$ to the abscissa axis, is the result. The only irregularity is among the smallest-bodied individuals (Fig. 1).

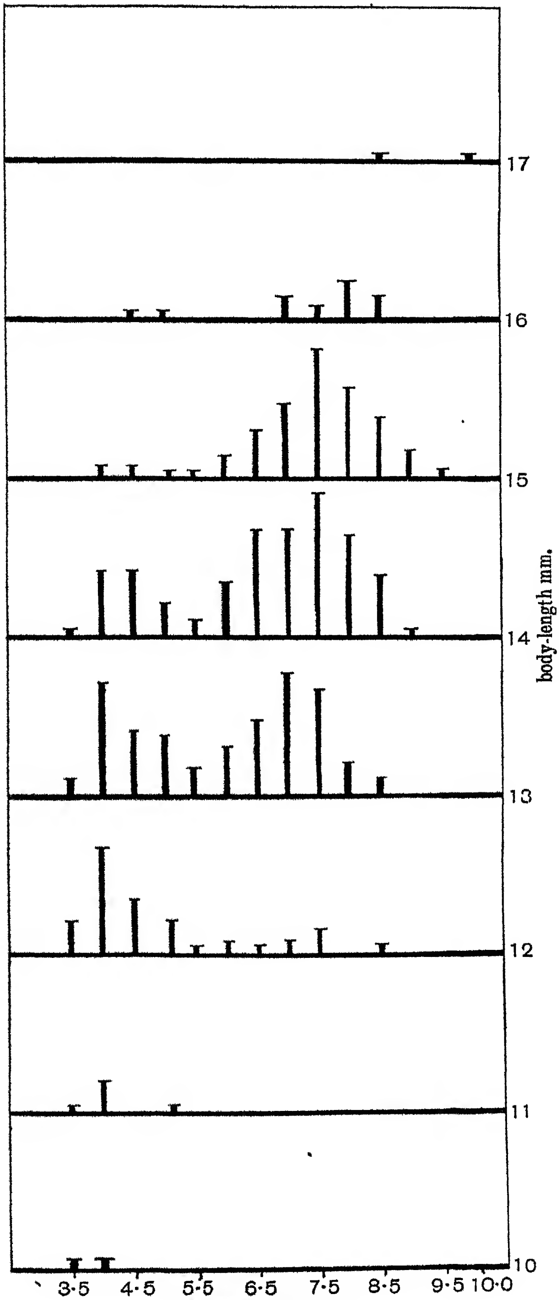
This indicates that if $y =$ *mean* forceps length and $x =$ body-length, then $y = bx^k$, where b and k are constants. This is the same relation that I have found to obtain between various heterogonic organs and the rest of the body (Huxley, 1924, and papers in press for the *Brit. Journ. Exp. Biol.*). Here, as measured by the angle of slope of the curve, $k =$ about 1·6. (In Fig. 5 it is greater, being about 2·0.)

On the other hand, it will naturally be objected, this "mean forceps-



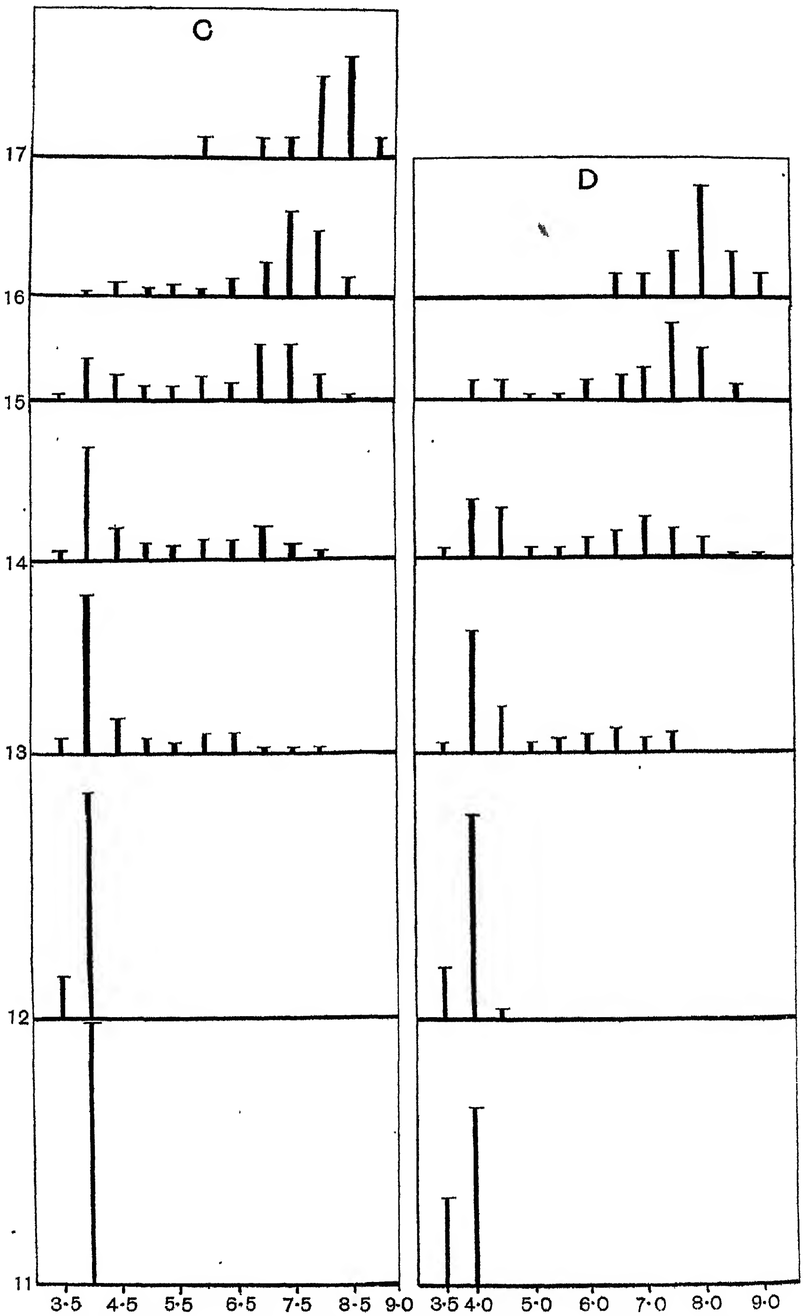
(A) Percentage frequency under favourable (*C*) and unfavourable (*D*) conditions.

Fig. 1. *Forficula* ♂, frequency of forceps-



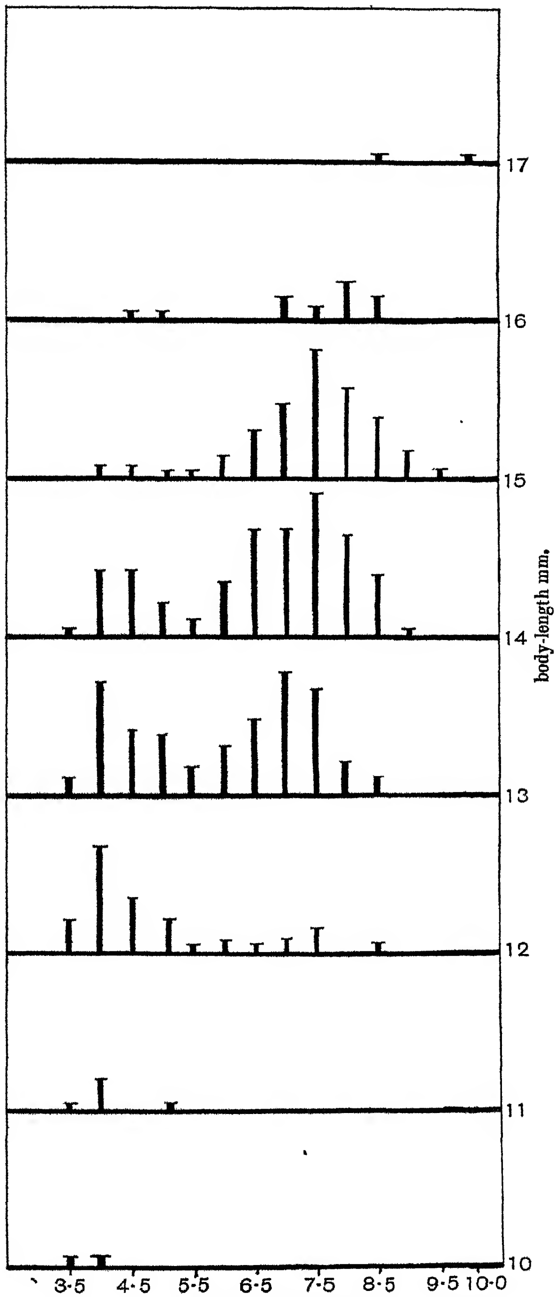
(B) Absolute frequency in another random sample of 445 specimens.

length for each 1 mm. body-length class.



(A) Percentage frequency under favourable (*C*) and unfavourable (*D*) conditions.

Fig. 1. *Forficula* ♂, frequency of forceps-



(B) Absolute frequency in another random sample of 445 specimens.

length for each 1 mm. body-length class.

length" has only a statistical significance in a bimodal assemblage such as the forceps; it has no physiological meaning, since the mean is close to the point of lowest frequency. I would suggest, however, that it has a meaning, and one which supports Diakonov's conclusion. The imaginal forceps of the earwig is definitely enlarged in the male sex, just as are, *e.g.* the mandibles of ♂ *Lucanus*, etc. Further, the disproportion is only produced at the last moult. I may therefore perhaps be permitted to advance the following provisional hypothesis. The male forceps is essentially a heterogonic organ. The straight line curve in Fig. 2 represents its *theoretical* relative growth-curve, which would make

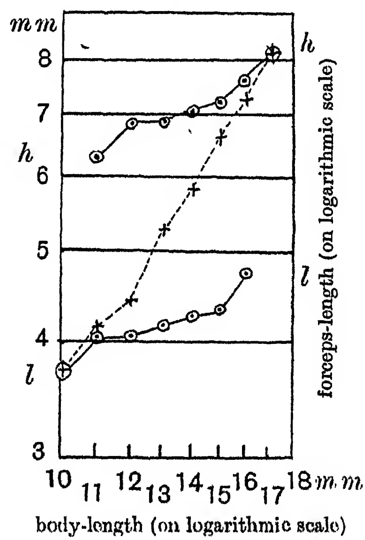


Fig. 2. *Forficula* ♂, logarithmic plot of means of lengths of "high" forceps (*h*—*h*), "low" forceps (*l*—*l*), and all forceps (dotted), against body-length, for 1519 specimens (series *A*—*E* inclusive).

it stand in a simple exponential relation to the rest of the body. We must suppose further, however, that the affair is complicated by the existence of "equilibrium-positions" such as Djakonov postulates. The great majority of individuals are thrown off from a mean position on the primary curve, into mean positions near the two modes actually observed. When the body-length is small, very few are thrown to the *m*-type mode; but the number of these increases with increasing body-size, until finally all are of this type. The conception becomes clearer when Figs. 1 and 2 are further examined. In addition to the total means, the means for the *b*- and *m*-series are also plotted (as logarithms). It will be seen that for *both* series the curves for the major part of their course

make an angle of considerably *less than* 45° with the x-axis, indicating what we already noted previously, that here the forceps is *decreasing* in relative length: but that both the beginning and the end of both curves show a considerably greater steepness. This, I imagine, indicates a strong tendency for the forceps-length to remain very close to one or other equilibrium-position, in spite of considerable changes in body-size. When, however, the body-size is too much altered, whether up or down, the proximity of the equilibrium-position can no longer be held, and forceps-length changes abruptly.

In passing, it is obvious that additional factors of a modifying nature must also be at work, for without these we should not find the m- and b-series overlapping, but discontinuously marked off round the two modes.

I do not see how the remarkably straight line of the curve for total means, together with the peculiar shape of both the curves for the single series, can be explained except on the assumption of an underlying mechanism for heterogonic growth (constant differential growth-ratio), complicated by the existence of equilibrium-positions.

The hypothesis of equilibrium-positions is strengthened by analysis of the figures for Groups C and D, of which, as already stated, C came from a normal habitat under the bark of tree-stumps, D from the wood-fibre in parts of the same habitat in which the bark had previously been stripped off. Djakonov (*l.c.* pp. 223–5) has shown that those from the wood-fibre were significantly smaller in body-length, pronotum-length, and mean forceps-length. He also showed that the relative number of b-type forms was markedly increased (from 46·15 to 62·50 per cent.) in the wood-fibre.

Of his specimens, 557 from bark (my Group C) and 341 from fibre (my Group D) were available for correlation purposes. When the mean forceps-length for all was taken, that for C was considerably larger than that for D. On the other hand, when the b- and m-type forms were separated from each other, not by adopting an arbitrary line of demarcation as done by Djakonov, but by the procedure outlined above (p. 313), of treating every assemblage of forceps-lengths for each body-length on its merits, I found that the differences between C and D were much less, when the b- and m-series were considered separately. The results are presented in tabular form.

	Group C mm.	Group D mm.	Difference in favour of C mm.
Mean of all forceps-lengths	5·69	5·43	0·26
Mean of all b-type forceps-lengths	4·19	4·12	0·07
Mean of all m-type forceps-lengths	7·14	7·10	0·04

This result is at first sight paradoxical. It becomes clear, however, on further analysis.

(1) We can tabulate the specimens of Groups *C* and *D* according to the percentage of the whole sample found (*a*) in each of the body-length classes, (*b*) in each of the forceps-length classes; (*a*) can also be treated by taking the percentage frequency of each body-length class

TABLE II.

Percentage of specimens in each body-length class at each forceps-length in groups C and D. (The modes of both series are printed in heavy type.)

	3·5	4·0	4·5	5·0	5·5	6·0	6·5	7·0	7·5	8·0	8·5	9·0
Group *C*.												
11	—	**100·0**	—	—	—	—	—	—	—	—	—	—
12	15·8	**84·2**	—	—	—	—	—	—	—	—	—	—
13	5·3	**59·0**	12·6	4·2	3·2	6·3	**6·3**	1·1	—	—	—	—
14	3·4	**42·0**	11·4	5·7	4·0	6·3	6·3	**12·0**	5·7	2·3	—	—
15	1·2	**15·5**	9·3	4·3	4·3	8·1	6·2	**20·5**	**20·5**	8·8	1·2	—
16	—	1·1	5·3	3·2	4·3	2·1	6·4	13·8	**30·2**	24·5	7·5	—
17	—	—	—	—	—	7·7	—	7·7	7·7	30·8	**38·5**	7·7
Group *D*.												
11	33·3	**66·7**	—	—	—	—	—	—	—	—	—	—
12	19·3	**77·0**	3·8	—	—	—	—	—	—	—	—	—
13	3·4	**45·5**	17·0	3·4	4·5	6·8	**8·0**	4·5	6·8	—	—	—
14	3·2	**21·8**	18·5	3·2	3·2	6·4	9·7	**14·5**	10·5	7·3	0·8	0·8
15	—	**7·1**	**7·1**	1·8	1·8	7·1	8·9	12·5	**28·5**	19·7	5·4	—
16	—	—	—	—	—	—	8·3	8·3	16·7	**41·7**	16·7	8·3
17	—	—	—	—	—	—	—	—	—	—	—	—

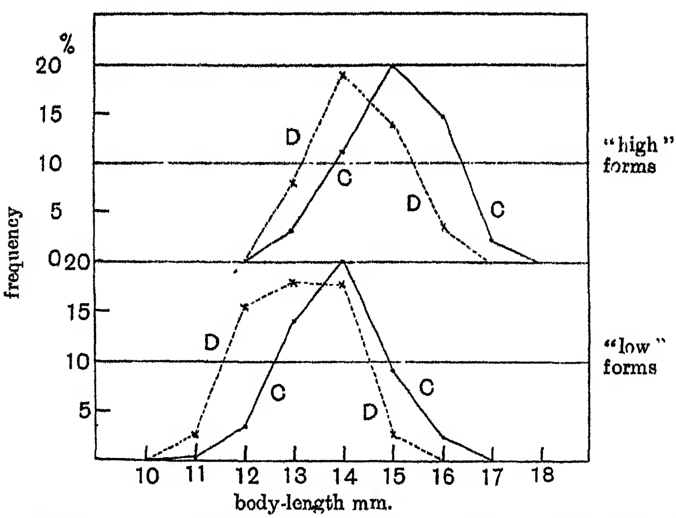


Fig. 3. *Forficula* ♂, change in percentage frequency of body-lengths with change from favourable (*C*) to unfavourable conditions (*D*).

within the *b*- and *m*-series separately. The results for body-length are given in Table II and Fig. 3. It will be seen that the previously-mentioned decrease of the mean body-length in *D* is due to a marked shift of the mode and indeed of the whole frequency-curve. Group *D* includes individuals of a body-length class below the lowest found in *C* (save for one specimen of *C*), but its largest specimens are one class below the largest of *C*. Precisely the same holds good for the curves of the *b*-type specimens, and essentially the same for those of the *m*-type.

When, however, we examine the curve for frequency of the forceps-length classes (Fig. 4), we find quite other relations. Here there

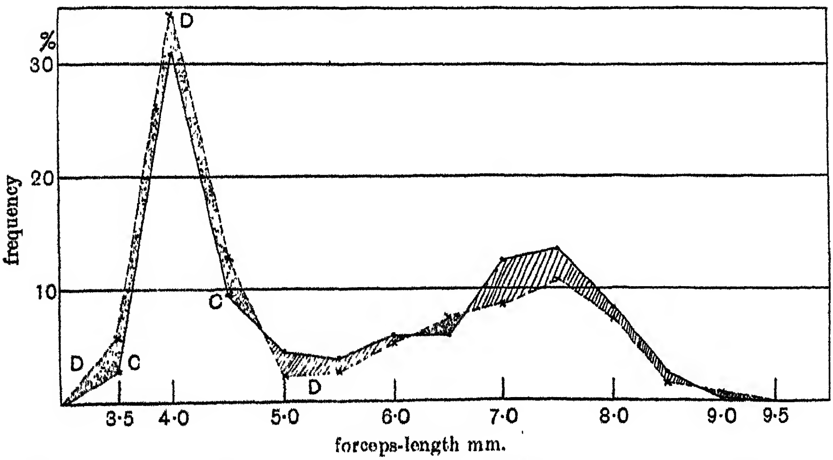


Fig. 4. *Forficula* ♂, change in percentage frequency of forceps-lengths with change from favourable (*C*) to unfavourable conditions (*D*). (517 and 341 specimens respectively.) Dotted area = region where the frequency of *D* is greater; striated area = region where the frequency of *C* is greater.

is no shift of the mode of *D*. The only significant alteration is in the frequency of individuals in different parts of the bimodal curve,—a shift which of course is most noticeable near the modes. There is a greater percentage frequency of *D* individuals at all lower forceps-lengths (from 3·5 to 4·5 mm. inclusive), and a greater frequency of *C* individuals at all higher forceps-lengths (with the exception of a small irregularity in the class of 6·5 mm.). The greatest preponderance of *D* over *C* is at 4·5 mm., one class above the low mode, the greatest preponderance of *C* over *D* is at 7·0 mm., one class below the high mode: this is the reverse of what we should obtain if the *D* curve were shifted bodily towards lower values, as occurred with the body-length curve.

Finally, the double-logarithmic plot of the lengths of the mean forceps, the mean *b*-type forceps, and the mean *m*-type forceps, all against body-length, both for *C* and for *D*, reveals further points of interest (Fig. 5).

We see that in every case where there are points both for *C* and *D* for the same body-length, they are higher for *D* than for *C* (with the statistically negligible exception of the point for *C* at 11 mm. body-length, which represents only a single individual). On the other hand, all three curves for *D* stop one body-length class below those for *C*.

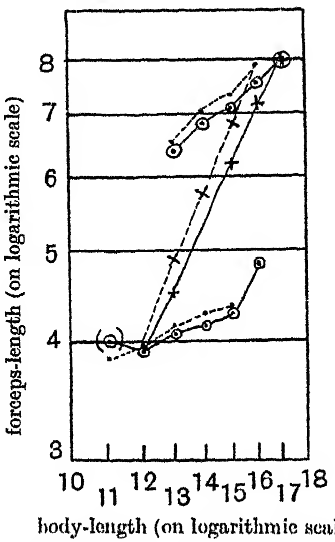


Fig. 5. Data for series *C* and *D*, plotted as in Fig. 2. Unbroken lines, *C*; dotted lines, *D*.

This is important. It shows that the higher values found for the forceps-length of *C* are due almost entirely to the absence in *D* of individuals, both in the *b*- and *m*-series, of the highest body-length. As already pointed out for other groups, these largest individuals in both series show a disproportionate rise in forceps-length as compared with more modal specimens; and this is also seen in the end points of the *b*- and *m*-curves for *C*. Thus the decrease in body-size in *D* has led to the disappearance of disproportionately large forceps both in the *b*- and *m*-type series, with consequent marked lowering of the mean. Not only that, but it has led to what is still more important for the lowering of the mean forceps-length, namely a throwing of a larger percentage of individuals into the *b*-type.

The paradoxical fact that for each body-length at which both *C* and *D* are represented, the forceps-length is higher for *D*, can only, so far as I can see, be explained on the idea of alternative equilibrium-positions. In the normal curve, *e.g.* for *C*, or for *A*, the failure of the orceps with increasing body-size to increase in length as rapidly as the body (relative decrease of forceps-length) in the central portions of the curves for both *b*- and *m*-series, was above ascribed to the existence of two equilibrium-positions of absolute forceps-size into which the forceps could most easily grow. In Group *D*, we may reasonably suggest that the effect of unfavourable conditions on stunting the body-size has, in the same way, not been able to exert a corresponding effect upon the forceps. Accordingly, in Group *D*, some of the individuals in each body-length group would, but for the stunting, have been in the next higher class; and their forceps-length still approximates in some degree to what it would have been if they had not been stunted. In this connection it is perhaps of significance that the divergence between the curves for the separate *b*- and *m*-series of *C* and *D* is greater for the *m*- than for the *b*-series, and that it increases within the *m*-series with increasing body-size.

The apparently total disappearance in Group *D*, among the *b*-type individuals, of those with large body and disproportionately large forceps is interesting, but also puzzling.

The remainder of the Groups (*A*, *B* and *E*) may also be compared with each other and with *C* and *D* along similar lines. It should, however, be remembered that the comparison cannot be so rigorous, as they come from more than one locality and were collected in more than one season: but in general the results support our contention. Thus the range of variation (for all the Groups, *A* to *E*) of the mean forceps-length of the *b*-types is 0·29 mm., or only 6·9 per cent. of the mean forceps-length of the total. Similarly, that of the mean forceps-length of the *m*-types is 0·44 mm. or only 6·1 per cent. of the mean for the total. However, the range for the mean forceps-lengths of the *b*- and *m*-types together for each of the five groups is 1·01 mm., or 17·4 per cent. of the mean for the total. The range for mean body-length is 1·75 mm. in the five groups, which is 12·6 per cent. of the mean body-length of the whole population. Finally the range in the percentage of the *m*-types within the five groups is no less than 26·1 per cent., which is 48·4 per cent. of the mean for the whole. Thus once more a given change in body-length will be correlated with a less-than-proportional change of forceps-length in either of the *b*- or *m*-series taken separately. It will,

however, be associated with a large change in the percentage of *b*- and *m*-type forms respectively, which will of course bring with it a considerable change in the mean forceps-length for all specimens ($b + m$ together).

For some reason which only experimental analysis could reveal, Group *A*, with lower mean body-length than *C*, had a considerably higher percentage of *m*-types, and Group *B*, with the lowest mean body-length, had a higher percentage of *m*-types than *C*, *D*, or *E*. In general, however, the conclusions I have come to appear to explain the facts, at least qualitatively.

When the percentage of *m*-types is calculated for each body-length class (Table I, last column), what at first seems a paradox is found (Fig. 6): the groups with low mean body-length show in general a

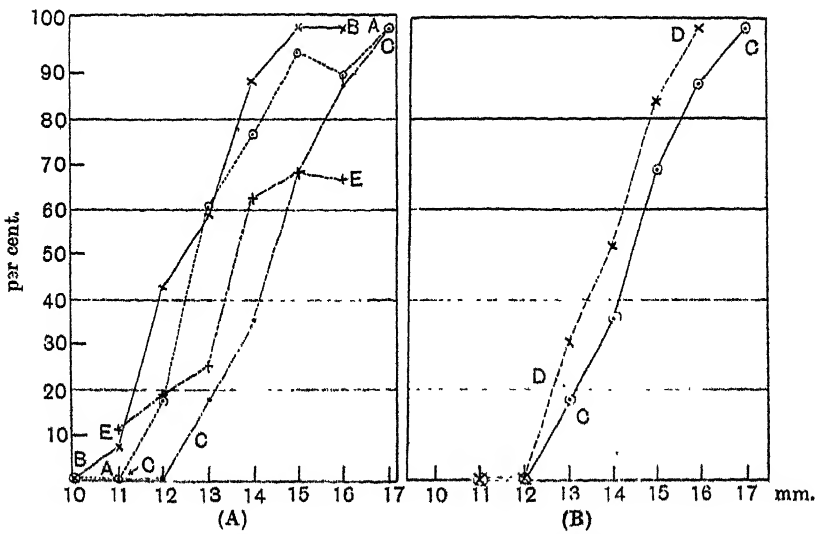


Fig. 6. Percentage of *m*-types at each body-length (A) for groups *A*, *B*, *C*, *E*; (B) for groups *C* and *D*.

higher percentage of *m*-forms in each body-length class. This is well seen for *D* as against *C* and in *B* as against *A*. *C*, with the highest mean body-length has the lowest *m*-percentage throughout, and *vice-versa* for *B*. This doubtless has a similar explanation to the paradox discussed on p. 323 with regard to the relation of mean forceps-length to body-length classes. First, the groups with low mean body-length have no individuals in the highest classes (and *vice versa*); and secondly,

the reduction of body-length does not exert a *proportionate* reduction of forceps-length. In the groups of low mean body-length, there will be fewer individuals left in the high body-classes, and these will be predominantly those with the strongest tendencies towards developing "high" forceps.

From our curves, however, we can prophecy that all male earwigs with body-length of 17 mm. or over will be entirely of *m*-type; that there will be 80 per cent. or more *m*-type in those of 16·5 mm. body-length (the last point for *E* is based on a total of three individuals only). Two-thirds or more of earwigs of body-length 15 mm. and half or more of those of body-length 14·5 mm., will be *m*-type. *Per contra*, half or more of those below body-length 12·5 mm. will always be of *b*-type, and two-thirds or more of those of body-length 11·75 mm. At just below 11 mm., 90 per cent. or more will be of *b*-type, and those of 10 mm. will all be of *b*-type. It may be regarded as likely that the observed geographical and annual variations in the percentage of "low" and "high" males in large samples will be mainly due to conditions which affect absolute size. (As Brindley and Bateson (*l.c.*) and Brindley (1914 *a*) have pointed out there is a very large variation in the percentage of high forms from different localities. Only 3 per cent. of the males from a Cambridge collection, but nearly 60 per cent. of a Faroe Island collection, were "high." In some of the Scilly Islands, the preponderance of high males is even greater, while in other localities they are wholly absent.) Bateson and Brindley themselves drew attention to the general relation existing between large body-size and "high" forceps, but did not apparently see that it could be used to explain the place variations; and neither they nor Djakonov discovered the regularity of the relation between mean total forceps-size, *b*- and *m*-series forcep-size and body-size.

I think that it may be fairly stated that this analysis takes Djakonov's important work a step further, and makes still more probable the existence of "equilibrium-positions" for the development of the male forceps in *Forficula*. This is of some interest, since the existence of such modal possibilities for development is very rare in animals. The developmental physiology of such a condition must be of very great interest. I clearly realise, however, that only experiment, utilising both the methods of genetics and of developmental physiology, can finally clear up the situation. I would wish to conclude by renewed thanks to Dr Philiptschenko.

SUMMARY.

1. Djakonov had come to the conclusion that the bimodality of forceps-length in male earwigs (*Forficula auricularia*) was not due to genetic differences, but that the "low" and "high" types of forceps represented favoured equilibrium-positions for the development of the forceps.

2. Further analysis of Djakonov's original (unpublished) data has confirmed this view. The chief results are as follows:

(*a*) The largest body-length classes in a given natural sample of earwigs contain only "high" forceps, the smallest only "low" forceps, but all the intermediate classes show bimodality.

(*b*) If the logarithm of the mean forceps-length for all forceps in each body-length class be plotted against the logarithm of the mean body-length, a good approximation to a straight line is obtained (Fig. 2), indicating that the fundamental growth-mechanism for the male forceps is similar to that found for other heterogonic organs, viz. $y = bx^k$, where y = organ, x = rest of body, and b and k are constants, k being > 1 for positively heterogonic organs such as the forceps.

(*c*) If, on the other hand, a similar plot is made for the mean forceps-length of the "low" and "high" forceps-series separately, a curve is obtained which, over most of its extent, indicates a similar mathematical relationship, but with $k < 1$: at both ends of each curve, k is larger ($=$ or > 1). This indicates that with changing body-size the forceps-size tends to stay near its modal value as long as possible, finally changing rapidly when the body-size becomes too large or too small.

(*d*) This is confirmed by the analysis of two groups (*C* and *D*) of which *D* was made to live under unfavourable conditions. This brought about a decrease in mean body-size of over 1 mm.; but the mean "low" forceps-size was only decreased by 0·07 mm., the mean "high" forceps-size only by 0·04 mm. Further, although the two modes for "low" and "high" forceps were thus hardly changed, the percentage numbers of individuals grouped round each mode were notably altered; *e.g.* the percentage of "high" forceps-type individuals was reduced from 51·1 to 44·0 by the unfavourable conditions.

3. In general it appears that the cause underlying the bimodality of the forceps in the male earwig is to be sought in the field of developmental physiology.

(*a*) There appears to exist a typical heterogonic mechanism of the ordinary type.

(*b*) This is obscured by the existence of two equilibrium-positions into one or other of which the developing forceps can most readily fall.

(*c*) Finally, the most obvious effect of increasing body-size is the transfer of increasing numbers of individuals from the "low" to the "high" equilibrium-position. This is combined with a slight increase in the value of the mode and of the mean of both the equilibrium-positions, the net result being that the mean value for forceps-length remains at its theoretical value bx^k, although this mean is far from either of the two modes, and may even fall at a size actually not exhibited by any actual forceps.

4. From an analysis of the facts under 2 (*c*), the limiting percentages of "low" and "high" males for given body-size classes can be prophesied. *E.g.* male earwigs of less than 11 mm. body-length will contain 90 per cent. or more of forms with "low" forceps, while at least two-thirds of those of 15 mm. body-length will be of "high" forceps-type. Those of 10 mm. or less will be all "low," those of 17 mm. or more, all "high."

5. The observed geographical and annual variations in percentage of "high" and "low" forms may thus be expected to depend on conditions influencing absolute body-size. However, only experiment, utilising a combination of genetic and developmental methods, can finally solve the problem in detail.

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A GENETIC STUDY OF GREEN-VARIEGATED YELLOW LEAVES IN THE JAPANESE MORNING GLORY.

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(With Five Text-figures.)

CONTENTS.

INTRODUCTION.

IN looking over the old books on the Japanese morning glory, *Pharbitis Nil*, we often find the illustrations of half green and half yellow[1] leaves growing on one plant, and also green and yellow leaves occurring alternatively on another. These forms of chimaera are known to us as "bicoloured leaf[2]" or "Matsushima leaf[3]" (Fig. 1). Besides these there is recorded and illustrated in our old books what is called "Matsushima-variegated" (Fig. 2), in which irregular bicoloured mosaics

[1] By "yellow," we mean not pure yellow, but yellowish green or *chlorina* type.

[2] In the classical books published in the years during the Bunka and Bunsei eras (1804–1829), this nomenclature was usually adopted, but afterwards this type was generally known as Matsushima leaf.

[3] In Iwasaki-Kanyen's *Sômoku-Sodategusa* (1833, 1–2, p. 31), an old Japanese book on plant breeding, the term "Matsushima leaf" was first applied to the yellow leaf having green variegation of the Japanese morning glory. This term seems, as some authors stated, to have derived from the analogous diversity in features of the bicoloured patterns of the plant to the multiform islets of Matsushima, a famous scenic place in North Japan.

Fig. 1. The so-called Matsushima specimen pictured in *Asagao-Sô* (1817). This and most other pictures of Matsushima forms given in the old books are more or less exaggerated and not quite true to nature.

Fig. 2. The so-called Matsushima-variegated leaf pictured in *Tohi-Syûkyô* (1857).

occur on the leaves. The writer had an incidental opportunity of studying these peculiar bicoloured leaves. The results of experiments showed that the mosaics are due to somatic mutations occurring on the yellow-leafed plants.

A HISTORICAL SKETCH.

The *Kadan-Asagao-Tsû* (1815), one of the oldest books on the Japanese morning glory, gives a coloured illustration of a specimen called "Chônotomo[1]." This specimen has normal leaves and dilute red flowers with crapy corollas and is evidently one of the so-called Matsushima-leafed individuals. The illustration represents a sectorial chimaera of the green and yellow parts, on most of whose leaves bicoloration is found, just one-half being green and the other yellow. In *Kengyû-Hinruizukô*, which was compiled about the same time as the above-cited book, we find a coloured sketch of a Matsushima-leafed specimen illustrated as a bicoloured leaf. The leaves of this specimen are all bicoloured in complicated mosaics of green and yellow. It blooms as dilute red. Another Matsushima-leafed specimen (Fig. 1), with maple leaves and blue double flowers, is represented in *Asagao-Sô* (1817). This specimen is a sectorial chimaera, all of the leaves displayed in the coloured picture being half green and half yellow. Two years later, *Kengo-Hin* (1819) was published. In it we find also a sketch of the Matsushima type bearing normal leaves and crapy corollas. A note reads that there are varieties of the Matsushima type, some normal and others narrow, with such corollas as funnel-shaped, cherry-flower-like, crapy, gentian-like, etc. According to this statement, the Matsushima type enjoyed great popularity at this period, and there were cultivated many races which appeared by new combinations of factors on natural crossing. Many more examples of the Matsushima and Matsushima-variegated leaves are recognisable when we study such books as *Asagao-Hanaawase* (1853), *Santo-Itchô* (1854), *Tohi-Syûkyô* (1857), etc., published during the eras of Kaei and Ansei (cf. Fig. 2). Such relatively prevalent cultivation of the Matsushima forms, however, came to an end after the Restoration of the Imperial power in 1868. The Japanese morning glory was much admired and cultivated in and after the era of Meiji (1868-1912) for the peculiar shapes and forms of its flower and foliage, but the existence of bicoloured leaves almost slipped from the memory of our cultivators.

[1] "Chônotomo" may be literally translated as "friend of butterfly."

THE RECOGNITION OF THE TYPE, ITS BEHAVIOUR AND HYBRIDISATION.

The writer produced by selection a pedigree strain bearing yellow cordate leaves and dilute magenta flowers, designated by GY, from among a mixed population obtained from a seedsman. On hybridising this race with NN, a pure pedigree strain characterised by green *Nandina* leaves and dilute purple corollas, an F_2 consisting of green and yellow leaves in the usual ratio, as was expected, was reared by tracing the following generation of the green-leafed hybrids. Contrary to expectation, two individuals making a sectorial chimaera of green and yellow colorations on the foliage were observed among the F_2 sister plants. These unexpected plants bore some entirely green leaves and some yellow ones, and still the leaves occupying their seats on the border of two forms showed longitudinal bicoloration. Unfortunately the writer made no further observations upon the yellow sisters of F_2, beyond noticing these two abnormal plants. Owing to the lack of special observation on the F_2 seedlings, where their occurrence might have been suggested at an earlier stage, the appearance of these two chimaeras came as a surprise. The key to the abnormal behaviour of the yellow leaf in this cross was first given by inspecting the F_3 seedlings, and confirmed by subsequent observations upon the successive stages of the plant growth. The appearance of green-yellow-chimaeras may be accounted for as a form of vegetative mutation. The writer, encouraged by a new fact bearing upon the yellow leaf, carefully examined the progeny of one of the parental pedigree strains. The yellow-leafed strain, GY, had been selfed since 1922, and gave one green exceptional plant in 1923. In 1924 close observation was made of the seedling bed of this strain, and some cotyledons having green variegation were found among the yellow seedlings. The observations, though few in number, are given in Table I.

TABLE I.

Pedigree	Green leaf	Green-variegated yellow leaf	Yellow leaf	Total
A	0	2	8	10
B	0	0	3	3
C	0	1	5	6
Total	0	3	16	19

From the green plant obtained in the preceding year, however, we had a mixed progeny of green and yellow seedlings, with one green-variegated yellow specimen among them. Table II contains the result thus gained.

TABLE II.

Pedigree	Green leaf	Green-variegated yellow leaf	Yellow leaf	Total
D	27	1	6	34
		7		
Expected from a 3 : 1 ratio	25·5	8·5		34

The segregation of green and yellow leaves practically corresponds to the usual simple ratio, indicating the green rogue to be heterozygous for the yellow leaf. Notwithstanding the fact that the plant is thus a heterozygote there is no evidence of hybridisation. The plant, therefore, must be regarded as a mutant, of which we shall give full discussion in a later section.

The Results of F_2, F_3 and F_4.

The true nature of the yellow leaf in this cross being brought, for the first time, to light in 1924, the F_2 records, as indicated in Table III, were straightforward except for the occurrence of the two sectorial chimaeras. Such chimaeras may be identified with the so-called Matsushima leaves, of which we gave a brief account at the beginning of this paper in calling the attention of the reader to the classical literature.

TABLE III.

Pedigree	Green leaf	Matsushima leaf	Yellow leaf	Total
1	45	2 (*A* and *B*)	9	56
2	23	0	7	30
3	33	0	10	43
Total	101	2	26	129
		28		
Expected from a 3 : 1 ratio	96·75	32·25		129

An F_3 was produced from 17 green and 4 yellow F_2 plants, 21 in all. The progenies of green F_2 are classified into two groups, viz. those breeding true to green, and those throwing the recessive forms. The recessives in this case do not all consist of pure yellow leaves, but in addition to these there often appeared green-variegated yellows and rarely green-yellow-chimaeras, the so-called Matsushima leaves. Four yellow-leafed F_2 gave the yellow offspring, which, however, contained a few green rogues, besides some Matsushima-variegated yellows and two Matsushima leaves. The summary of the F_3 data will be found in Table IV. The number of greens which bred true to the type was 9, while 8 threw the yellow forms. In all the observations of the latter, we found 1 sectorial Matsushima and 6 Matsushima-variegated leaves among

TABLE IV.

Character of F_2	Pedigree number	Green leaf	Matsushima leaf	Matsushima-variegated leaf	Yellow leaf	Total
Green leaf	Total of 9 families	113	0	0	0	113
	1	113	1 (*C*)	2	19	135
	4	10	0	0	3	13
	7	32	0	0	7	39
	10	3	0	0	1	4
	14	18	0	2	4	24
	15	20	0	2	4	26
	.16	5	0	0	1	6
	19	15	0	0	5	20
	Total	216	1	6	44	267
Yellow leaf	9	1	1 (*E*)	2	6	10
	13	2	1 (*D*)	3	18	24
	18	0	0	2	5	7
	21	0	0	0	2	2
	Total	3	2	7	31	43

51 yellow segregates, which thus form only 19·10 per cent. of the total, while the ratio was 21·71 per cent. in F_2. Both percentages are thus lower than the normal expectation. In the four yellow pedigrees we counted 3 greens in a total of 43, the rest being yellow. From these yellow-leafed F_3, an F_4 generation was grown on, the data obtained being represented in Table V.

There were observed actually a few green-variegated yellow seedlings, but they were included in the yellow class in the table, because the record was taken in the seedling bed. Three green seedlings appeared among 111 F_4 of yellow pedigrees; a proportion which is rather low compared with F_3.

TABLE V.

Pedigree number	Green leaf	Yellow leaf (contains Matsushima forms)	Total
9—1	0	5	5
—2	0	19	19
3	1	26	27
Total	1	50	51
13—1	1	18	19
—2	0	2	2
—3	0	4	4
—4	0	3	3
—5	1	3	4
—6	0	7	7
—7	0	15	15
—8	0	6	6
Total	2	58	60
Grand total	3	108	111

MATSUSHIMA-LEAFED INDIVIDUALS AND THEIR PROGENY.

In Fig. 3, one of the Matsushima-leafed plants, which appeared in F_2, is diagrammatically shown in a spiral form indicating the phyllotaxy. Divergence of phyllotaxy in the Japanese morning glory is two-fifths. The plant *A*, of the two chimaeras, has a mixture of about three-fifths of green, and *B* only one-fifth of its original yellow, the rest being converted into green tissue. Also the yellow tissue of the latter disappeared from

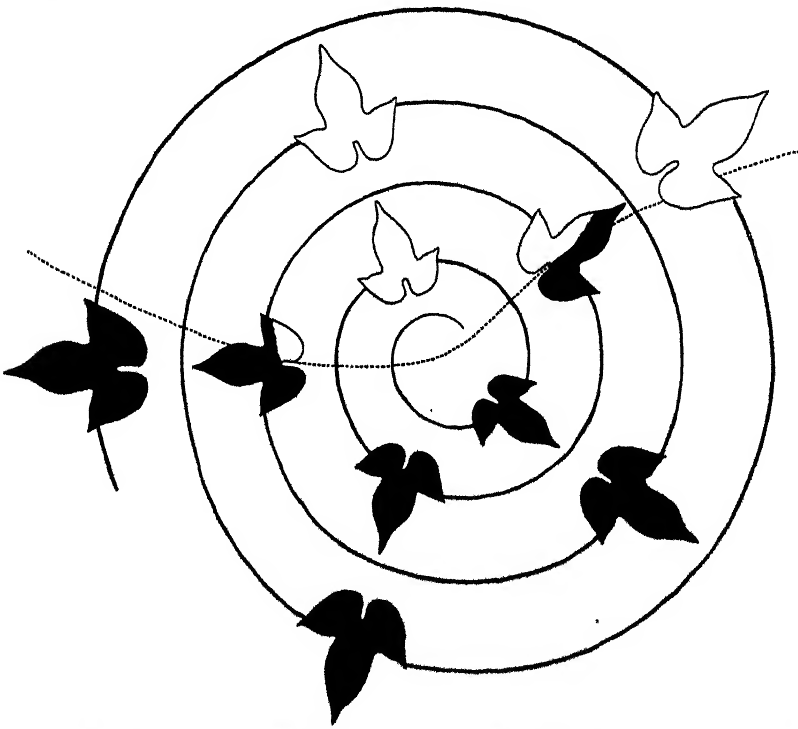

Fig. 3. The spiral diagram of a sectorially bicoloured specimen (plant *A*). The black part of leaves represents green and the white part yellow.

the upper part of the main stem, and afterwards the plant grew to be a green-leafed one. In both cases bicoloration coincided with phyllotaxy, and it very clearly shows the nature of sectorial chimaera. The Matsushima-leafed plants, *A* and *B*, gave few offspring, which, however, seem to be enough to represent the genetic nature of chimaeras, the results obtained being as given in Table VI.

Thus the two chimaeras segregated almost in the same manner; from the green part we obtained a small number of yellows among green-

TABLE VI.

Plant and part, from which seeds were obtained	Green leaf	Matsushima-variegated leaf	Yellow leaf	Total
A. Green part	7	0	3	10
Yellow part	1	2	5	8
B. Green part	9	1	2	12
Yellow part	0	0	3	3

leafed sisters, while the yellow part gave yellow leaves including a few Matsushima-variegated. Besides, one green individual appeared in the progeny of the yellow part of the plant *A*. The difference in the progenies between the green and the yellow parts of the chimaera-plants indicates a genetic differentiation of the much-discussed character, or in plain words the fact is accounted for by the transformation of the yellow leaf factor into a green leaf one in a vegetative tissue. The progenies of the green part of the plants *A* and *B* contained 6 yellows among 22 individuals, in a recessive proportion. From this ratio of segregation we can recognise that the yellow plants owe the genetic nature of the varied green part to one factor change. Consequently the tissues of the green part are heterozygous in constitution. Hence, the green-leafed F_3 plants should be composed of homozygotes and heterozygotes at the usual ratio. The raising of F_4 brought about the expected results as shown in Table VII.

TABLE VII.

Pedigree number	Green leaf	Yellow leaf (contains Matsushima forms)	Total
3	8	0	8
1	10	2	12
2	5	1	6
4	7	2	9
5	15	5	20
Total	37	10	47

As the records were taken by observation on the seedling bed, the green-variegated plants were counted together with the yellows. Out of five families, excepting the one which may be regarded as homozygous, all segregated yellow seedlings approximately in the expected ratio, the actual proportion being 21·28 per cent.

A further statement will be made of three Matsushima leaves, which appeared in F_3. One of them, the plant *C* obtained in pedigree 1 was a sectorial chimaera, while the plant *D*, which appeared in pedigree 13, turned out to be a periclinal chimaera. The former plant contains about

three-fifths of mutating tissues, as is diagrammatically shown in Fig. 4, and on the upper part of the main stem the tissue was entirely replaced by the prevalent green cells. The progenies of the green and yellow parts are recorded in Table VIII.

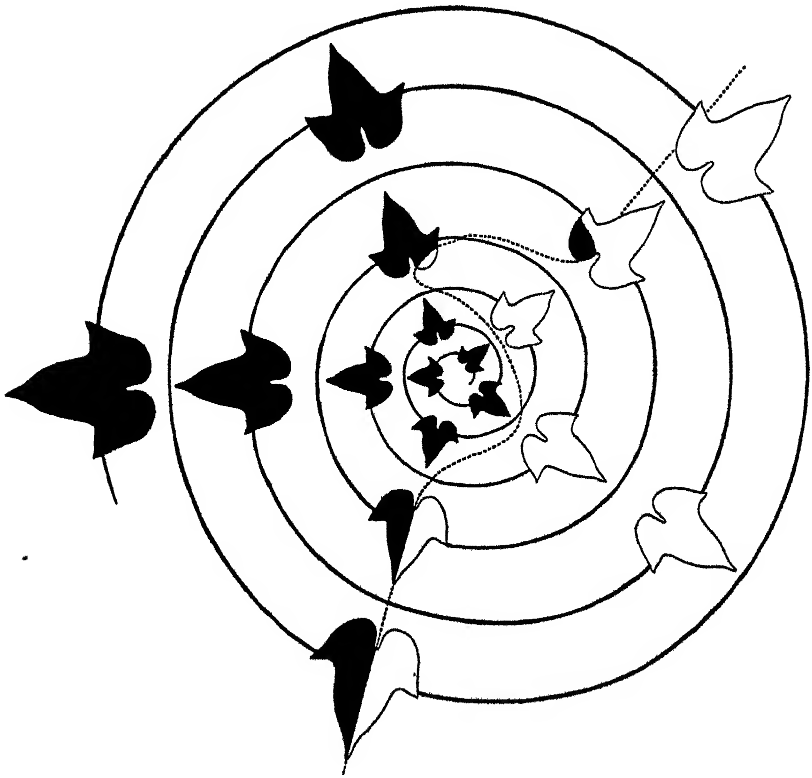

Fig. 4. The spiral diagram of another sectorially bicoloured specimen (plant *C*).

TABLE VIII.

Part from which seeds were obtained	Green leaf	Yellow leaf (contains Matsushima forms)	Total
Green part	10	3	13
Yellow part	0	5	5

As the census was taken by observing the seedlings, the green-variegated yellows were reckoned with the yellows. The result showed, as was expected from previous experience, that the green part of a

sectorial chimaera was produced by a factor mutation of yellow into green, giving heterozygous tissues. The point *D* bore yellow leaves of a similar pattern with a yellowish green patch at the centre. A microscopic examination of the section of the leaves showed a periclinal constitution of green and yellow layers, a yellow skin covering over a green core. Owing to the regular development of the plant tissues, the periclinal condition was maintained throughout the plant growth, as far as the writer's observation went. As the sub-epidermal layer of the plant tissues is composed of yellow cells, the subsequent generation might be expected to breed true or nearly so. The progeny of this periclinal plant was raised, and our actual examination of 21 individuals showed all to be yellow seedlings, except one green. A word may be added on the origin of this rogue. As was already stated, our yellow-leafed plants sometimes threw green individuals, and the green just mentioned is to be considered as having the same origin as the other greens.

Of the figures given in the old books, the one illustrated in *Tohi-Syûkyô* (1857) seems to be a periclinal chimaera of the Matsushima leaf, the yellow leaves, as in the plant *D*, having a greenish centre.

The plant *E* was an extreme type of the Matsushima leaf, and practically it is a green plant. A statement on this plant will be given in the next section.

GREEN MUTANTS.

The four F_2 yellows, as shown in Table IV, produced, in addition to yellows, a few greens. These green rogues may be considered as a result of either gametic mutation or somatic transformation of a factor in the tissues of the mother plants. In addition to these possibilities may be suggested another which will account for the origin of green rogues. Somatic mutation may occur in the embryonic stage or early growth of the seedling, and the mutated tissues, overcoming the prototypic yellow part in development, may produce greens. This is no mere speculative suggestion. Actually the plant *E*, which appeared in pedigree 9 of F_3 (see Table IV), had only a yellow patch on the lobe edge of its cotyledon, the rest of which, including the growing point of the bud, was entirely green and the plant afterwards grew up to be a green specimen. Of course the plant *E* was characterised by somatic mutation in the early stage of its embryonic development, and the prevalent growth of green tissues formed by the multiplication of a mutated cell must have caused the appearance of such a practically green plant. An

attempt was made to raise the F_4 generation with three F_3 specimens, two pure green rogues and one practically green one (plant *E*) to ascertain their genetic conditions. The results obtained are shown in Table IX.

TABLE IX.

Pedigree number	Green leaf	Yellow leaf (contains Matsushima forms)	Total
9—*a* (*E*)	25	7	32
13—*a*	8	2	10
—*b*	17	4	21
Total	50	13	63
Expected from a 3 : 1 ratio	47·25	15·75	63

The segregation of greens and yellows agreed nearly with a 3 : 1 ratio, the recessive proportion being 20·63 per cent. Whatever the origin of the greens which appeared among the yellows might be, their genetic constitution thus proved to be heterozygous, as far as the experiments were concerned. The average proportion of the green rogues among the Matsushima-lined yellow families is about 3·5 per cent. (the data, with which this calculation is made, are collected from Tables I, IV and V).

Hagiwara (1926) has lately reported a case of yellow leaves habitually throwing some greens. Such green-throwing yellow leaves may be identified with our Matsushima-lined yellows, but Hagiwara did not describe the occurrence of bicoloured leaves, notwithstanding the fact that he reared families from yellows which contained a high proportion of green rogues. As the writer has stated in other papers (Imai, 1924, 1925), the eversporting phenomena of the Japanese morning glory observed in several cases of different characteristics accompany vegetative variation in the same direction, as is also the case in the other plants such as de Vries' striped snapdragon, Emerson's variegated corn, Blakeslee's dwarf *Portulaca* and so on. Hagiwara's case, therefore, seems to be in need of thorough examination from this point of view. He also suggests the possibility of the occurrences of mutation in the green leaf factor to its recessive yellow allelomorph, but the evidence offered by him seems to stand on a rather insufficient basis.

Behaviour of the Factor for the Matsushima-Lined.

From the experimental data so far obtained, we can safely conclude that green on the Matsushima forms is due to the difference of a single

factor from the other prototype in its genetic relationship. And the only difference between the Matsushima and Matsushima-variegated leaves lies in the size of area of the green mutated tissues, and the area is determined by the point of plant growth, at which mutation occurred. When, for instance, it takes place in a cell of the growing point of the stem, a Matsushima leaf may come out, but in other cells, the production results in the Matsushima-variegated leaves. An analogy is seen in the variegated *Mirabilis* (*variegata*), with which Correns (1909) worked. *Variegata* is a green-variegated yellow- (*chlorina*) leafed specimen, variegation occurring always so definitely in every individual that Correns regarded the form to be due to a *variegata* factor. In the Japanese morning glory, however, the characteristic of *variegata*, or Matsushima variegation appears in only a few individuals among apparently pure yellow sisters. To what cause is this difference due? The writer is of the opinion that the *variegata* of *Mirabilis* is due to a factor which gives mutations of yellow into green as it occurs habitually in the Matsushima-lined yellows of the Japanese morning glory, the only difference between these two plants lying in the frequency of mutability. Vegetative mutations occur so much more frequently in *Mirabilis* than in the Japanese morning glory, that in the former all the individuals obtained were variegated. And both *variegatas* give a few green mutants.

The next problem to be solved is the allelomorphic relationship of green, Matsushima yellow and ordinary yellow. In *Mirabilis*, Correns presumed two factors to account for their relationship, besides a ground factor, because the three forms do not constitute a series of multiple allelomorphs. In the Japanese morning glory, the green leaf always behaves as a simple dominant to the yellow, and the Matsushima and yellow forms are transmitted as a recessive to green. But we have no data for determining the further relationship. The study of the genetic behaviour of Matsushima forms suggests some difficulty, because only a few plants assume the characteristic of variegation though they all carry a factor for the type. If the genetic cause of the Matsushima-lined is due to a modification of the yellow leaf factor, we should have a triple series of allelomorphs of green, Matsushima-lined yellow and ordinary yellow. But if it is not a case of multiple allelomorphs we may have to presume another factor governing the mutability, besides the yellow leaf factor. The final determination will be left for a future study.

The Mutability of the Matsushima Factor.

We had only a few green-variegated leaves among the offspring of the Matsushima-lined yellows, most of the rest being apparently pure yellows. Of 59 (3 green mutants omitted from this calculation) offspring of the Matsushima-lined yellows (the data taken from Tables I and IV), we recognised 12 Matsushima forms, *i.e.* about 20 per cent. In short, one-fifth of the yellows carry mutated cells in their bodies, while the rest remain in their prototypic condition. In these calculations, we neglected the green mutants. If these are produced by vegetative mutation in their embryonic stage after fertilisation, and so grow up to be apparently green ones owing to the predominant growth of the mutated tissues, the value may become larger than the figure above given. The calculation is based on so meagre a number that we cannot attach much importance to it, but it is to be recognised that the conditions are different from the case of Correns' *Mirabilis*. In *Mirabilis*, the green-variegated yellows stand at 100 per cent., while they form about 20 per cent. in the Japanese morning glory. We are presuming that the present cross is concerned with the monohybrid segregation of allelomorphs for the green and the Matsushima-lined yellow leaves, though there is no definite evidence for this. If, however, the case is dihybrid and contains some ordinary yellows the frequency as calculated above must increase.

On the Segregating Ratio.

The segregating ratio of the green and the yellow leaves in the offspring of the heterozygous greens or the green part of the Matsushima leaves is generally lower than expected. When we make a total of such data (the data taken from Tables II, III, IV, VII and IX) we have 431 greens and 109 yellows (the latter including the Matsushima forms) out of the total number of 540. The proportion of the yellow leaves is only 20·19 per cent., where we expect 25 per cent. The yellow specimens being generally somewhat weaker than the green, it is no rare matter in ordinary cases to observe some discrepancy in the segregating ratio of the green and the yellow leaves. The above low ratio may be partly accounted for by such a cause, but we must not lose sight of the ever-sporting nature of Matsushima-lined yellows, owing to which the number of the yellow segregates will tend to decrease.

THE ORIGIN OF THE MATSUSHIMA-LINED.

The fact that the occurrence of Matsushima or Matsushima-variegated leaves is found in the books published one hundred and ten years ago[1] shows that the characteristics of those variations were recognised in the beginning of the extensive cultivation of this plant. The yellow leaf, which is now very commonly found in our gardens, however, was as rarely visible at that time as the Matsushima forms. Though the phenotype of the leaf colour of the Matsushima-lined yellow was yellow, it was genetically different from the common yellow. Now we wish to determine whether the old yellow leaves are the true yellows or the Matsushima-lined ones.

The existence of the Matsushima forms gives a chance of obtaining the yellow leaves, because the former throw the latter in a high proportion in their offspring. The authors of the old books unanimously denied any certainty in the breeding behaviour of the Matsushima forms. For instance, the author of *Kadan-Asagao-Tsû* (1815) states that the green-variegated leaves appear irregularly among the offspring of the yellows, and the mono-chromatic leaves are precariously produced from the green-variegated yellows. The author of *Kengo-Hin* (1819) arrived at the same conclusion. He says in effect: "The Matsushima forms are produced occasionally from yellows, but the seeds of the Matsushima leaves do not always give similar offspring, only a few Matsushima forms being obtainable among many sisters." His argument went a step further towards recognition of the fact that the Matsushima characteristics are inheritable. In the identification of the old yellows we must keep such breeding behaviour of the Matsushima forms in mind.

In both *Kadan-Asagao-Tsû* (1815) and *Kengyû-Hinruizukô* (1815), there are some descriptions of the yellow and the Matsushima leaves, such as the following:

	Yellow leaf	Matsushima leaf
Kadan-Asagao-Tsû	1. Normal leaf, funnel-shaped flower with dilute blue corolla	1. Normal leaf, dilute red crapy corolla
Kengyû-Hinruizukô	2. Normal leaf, dilute red crapy corolla	2. The same as above
	3. Normal leaf, funnel-shaped flower with dilute red corolla	
	4. Normal leaf, funnel-shaped flower with dilute blue corolla	

The yellow leaf, which was illustrated in *Kadan-Asagao-Tsû*, is the same as one of the three specimens listed in *Kengyû-Hinruizukô*, and

[1] Since the importation of the seeds of the Japanese morning glory from China, over a thousand years have elapsed, but the period during which the plants were grown extensively with abundant variations extends little over one hundred and ten years.

further, both books give similar Matsushima leaves. The Matsushima and the yellow leaves were rarely found in those days, and these traits seem to have made their first appearance some years before the publications of these books. Two years later, *Asagao-Sô* (1817) and *Teichû-Asagao-Fu* (1817) were printed. The former has a list of over five hundred forms[1], among which we find several yellow and Matsushima leaves as follows:

Yellow leaf	Matsushima leaf
1. Maple leaf, split flower with dilute blue-spotted corolla (specimen not listed, but given in painting)	1. Maple leaf, split flower with spotted corolla
2. Maple leaf, split flower with spotted corolla	2. Maple leaf, irregularly split flower with dilute blue corolla
3. Normal leaf, funnel-shaped flower with intense blue corolla	3. Normal leaf, funnel-shaped flower with spotted corolla
4. Normal-formed, variegated leaf, funnel-shaped flower	4. Normal leaf, funnel-shaped flower

The description, though sometimes inadequate in the original, is accurate enough for the present consideration. In the books of 1815, the Matsushima and the yellow forms have been confined to the normal-shaped leaves, but now in this book we have two maple specimens each in yellow and Matsushima leaves, indicating a progressive step in evolution. And in *Teichû-Asagao-Fu* there is found a yellow-leafed specimen of a narrow willow leaf with narrowly split, dilute red flowers, which was less common in those times. The following table will give a comparison between the yellow and the Matsushima leaves as listed in *Kengo-Hin* (1819):

		Yellow leaf	Matsushima leaf
Leaf form	Normal	Present	Present
	Maple	,,	,,
	Pear	,,	Absent
Flower form	Funnel-shaped	,,	Present
	Crapy corolla	,,	,,
	Cherry-blooming	,,	,,
	Peacock-blooming	,,	Absent
	Gentian-blooming	,,	Present

In these three tables, we find a very close relationship in variation between the yellow and the Matsushima leaves. This circumstance may allow us to conclude that these yellows are not ordinary ones, which are expected invariably to breed true to the type, but that they are Matsushima-lined ones, which may produce some greens and Matsushima forms in their offspring.

The yellows are now almost confined to the ones which breed true

[1] The author of this book tells of the existence of over seven hundred forms at that time.

to the type, and the Matsushima-lined yellows have become very rare in our gardens. The cultivation of the Matsushima forms attained its zenith of prosperity in the period of Kaei and Ansei eras (1848–1859). But their cultivation fell off suddenly in the era of Meiji (1868–1912), giving place to the ordinary yellows. As stated in the foregoing pages the yellow leaf which first appeared was that of the Matsushima-lined. So, we may suggest the following two possibilities with regard to the phylogenetic relationship between the green, the Matsushima-lined yellow and the ordinary yellow:

(1) Green ↗ Matsushima-lined yellow
↘ Ordinary yellow

(2) Green → Matsushima-lined yellow → Ordinary yellow

The third possibility of green → ordinary yellow → Matsushima-lined yellow, must be rejected in view of the evolutionary history mentioned above. But we cannot decide which of the other two possibilities is the true one, because we have no key to solve this problem.

TRICOLOURED LEAVES.

In the Japanese morning glory, variegation usually means a green or yellow leaf with white or pale creamy patches, which condition is transmitted as a simple recessive to the monochromatic condition. From the fact that a variegated leaf is found as one of the popular characteristics in such books as *Asagao-Tsû* (1815) and *Kengyû-Hinruizukô* (1815), we may regard this as rather an old character. According to such literature, however, there was yet no variegated yellow leaf, the variegated leaves being all green. The occurrence of the variegated yellow leaf was first recorded in *Asagao-Sô* (1817). In *Kengo-Hin* (1819) we are given some description of this form. The author of this book when treating of the ornamental importance of the variegated yellows, said that this form is the best of the yellow leaves, which means practically the best among all leaves found in the Japanese morning glory. From this statement, we see that the cultivators of those days set a high value upon this type.

From the fact that variegation occurs in the yellow leaves, it is but natural that we find tricoloured leaves of green, yellow and white, or in other words, variegated Matsushima leaves. In the recent books on the Japanese morning glory, the term "tricoloured leaf" is often mentioned, but few have made actual observations on them. The author of *Asagao-Mizukagami* (1818) first pointed out a tricolour type, but he gave

Fig. 5. A tricoloured leaf pictured in *Tohi-Syûkyô* (1857).

no picture. In a list given in *Asagao-Hanaawase* (1853), we find tricoloured leaves. The oldest figures (Fig. 5) of this type are found in *Santo-Itchô* (1854) and *Tohi-Syûkyô* (1857). The writer has not yet actually observed a tricoloured leaf, and an experiment to obtain such a leaf by crossing is in progress.

The writer wishes to acknowledge his indebtedness to Professor K. Miyake, under whose direction his study was taken, to Mr K. Hashimoto for his warm encouragement so kindly given, and to Messrs B. Kanna and K. Tabuchi for their help in his experiments. He owes very much to Mr S. Takahashi who generously allowed him to study his old books. The expenses for the present investigations have been partly defrayed by a grant from the Imperial Academy.

SUMMARY.

1. The so-called Matsushima and Matsushima-variegated leaves of the Japanese morning glory are bicoloured in green and yellow. The study of such peculiar forms shows that they are yellow specimens in which occurs a somatic variation to green.

2. The Matsushima forms are obtainable among the progeny of yellows in the average proportion of about 20 per cent. Such yellow leaves cannot be phenotypically distinguished from the ordinary yellows, which always breed true, but difference lies in their genotypes.

3. The Matsushima-lined yellow leaf behaves as a recessive to green, and segregation takes place practically in a 3 : 1 ratio, where the recessive may contain some Matsushima and Matsushima-variegated leaves.

4. Three sectorial and one periclinal Matsushima leaves were observed in the hybrid progeny. The green part of the Matsushima leaves showed itself to be heterozygous for green and yellow, so the green tissues owe their occurrence to a single factor change. The periclinal plant had yellow sub-epidermal layer and gave almost all yellow offspring.

5. The Matsushima-lined yellows give a few green mutants in their offspring. A breeding experiment shows that they are heterozygotes of green and yellow.

6. By a close study of old literature we are able to conclude that the old yellow leaves are of the Matsushima-lined type, and not ordinary yellow. The common yellow, however, is a variety recognised rather recently.

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EXPERIMENTS ON THE GENETICS OF WILD POPULATIONS. PART I. GRASSES.

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(With Ten Text-figures.)

CONTENTS.

INTRODUCTION.

COMPARATIVELY little being known of the heredity and potentialities of plant populations the question of origin and distribution is a difficult one. The geneticist studies the manner in which characters are inherited under controlled conditions. The ecologist and the student of plant geography record the facts resulting from the effects of habitat. But until recently the connection of genetics and ecology has not been made prominent. To the authors of this paper the interrelation between wild environment and genetic constitution of the inhabiting forms appears to be of the greatest importance.

The work of Bonnier, Schimper, Massart, Warming and others has shown that the environment exerts a considerable effect upon the habitus-type of a plant. Massart for example was able to produce the water form, the land form, and the amphibious form of *Polygonum amphibium* by growing clones of one individual in the respective environments. The work of plant geneticists on the other hand has shown that the genetical constitution of the plant is a stable fixed and absolute quantity under many conditions. It is therefore necessary to consider in what manner plant species have arisen and grouped themselves into

the typical populations recognised by ecologists. If the geneticist is right in saying that there is little effect of the environment upon the genotype, it is necessary to discover in what manner the phenotype exhibited by a particular population has arisen and become distributed.

While the results of ecological experiments indicate that the environment has considerable control over the morphology of the plant, they do not show in what manner the potential variability of the characters has arisen. Plant species differ in their capacity to respond to the various environmental conditions, but there are a number of cases known in which one species is found in different environments in one part of the country, whereas in another part where similar environmental conditions exist the species is represented by only one environmental form. The geneticist would say that the genotypes of the two districts were different, and therefore in some localities several forms could be produced, while in others the potential variability of the species was not sufficiently great to allow of more than one type being formed.

We will now consider some experimental work on local populations of grasses which has been carried out at the Station of the Scottish Society for Research in Plant Breeding, Corstorphine.

Pollination of Grasses.

At the same time as the different species-populations were under observation, careful experiments were conducted to determine the mode of pollination for each species. The results of the investigations show that in the majority of the perennial grasses self-sterility is strongly in evidence, although in certain species individuals vary considerably in this respect, some attaining a self-fertility percentage equal to that of natural seeding. On the other hand, the majority of the annual grasses experimented with were self-fertile but were not necessarily self-pollinated in nature, owing to the anther-dehiscence of a flower taking place a few minutes later than the free exposure of the stigma.

The occurrence of self-sterility in a population is of importance in the study of wild populations, since in a highly self-sterile population the production of seed depends entirely upon cross-pollination. It is therefore necessary to state the following facts which prove the suitability of the methods employed in the study of the problem.

1. Plants which were self-sterile when artificially isolated under pergamine bags or specially constructed pollen-proof boxes, continued to be equally self-sterile when allowed to flower exposed under complete natural isolation—*i.e.* isolation by time of flowering. The plants so

isolated remained sterile only so long as foreign pollen was excluded, seeds being set whenever cross-fertile plants in flower were introduced into the same greenhouse.

2. When spikes or panicles on different self-sterile but inter-fertile plants were enclosed together in the same bag, the percentage of flowers setting seed equalled that of natural pollination.

3. *Avena fatua*, a species known to be self-fertile, was found to remain self-fertile under the artificial isolation of a bag or pollen-proof box.

4. When emasculated spikes or panicles of cross-fertile plants were cross-pollinated by hand and enclosed in a bag the percentages of seed obtained often reached 100 per cent.

5. In the self-sterile plants the pollen and ovules proved to be functional when compatible crosses were made.

After considering the data which have been collected at the Plant Breeding Station and the literature on the subject, it is extremely doubtful whether any definite conclusion can be drawn regarding the cause and inheritance of self-sterility in plants showing no true functional sterility. But it is evident that differences occur between different plant groups, so that data collected from any one species or variety are not necessarily applicable to another species or variety. Again, environment appears to exert a strong influence upon the behaviour of some self-sterile plants. There is however evidence that sterility has a genetical basis; and the results obtained from the work on grasses tend towards an hypothesis of a balance of conflicting physiological factors similar to that suggested by Goldschmidt to account for the facts in the case of *Lymantria*.

The grass breeding work at the Plant Breeding Station has involved the intensive study of several species of *Gramineae* of agricultural importance. This study soon revealed that within a single species there are great morphological and physiological differences between individuals. These differences were in many cases found to persist when plants were cultured for a number of years in an environment which was made as consistent as possible. Therefore it was thought desirable that the problem of the genetics of the plants should be studied in their relation to habitat.

Although a considerable literature exists dealing with the effect of the various environmental factors upon the individual plant, little has been published on the problem of the hereditary constitution of plant populations.

The results now given, being of a preliminary nature, are merely suggestive and indicate the possibilities of this line of research.

Lolium perenne. Many characters of this species were found to be highly variable. Some are influenced to a greater or less degree by environment and are therefore modifications. Others again are little influenced by environment and behave as variations. Material was collected both from wild and from commercial populations. The population whose genetical constitution was most worked out was taken from a coastal area. The plants were removed from their natural habitat to Corstorphine without any selection whatsoever. There, a few tillers of each plant were rooted in boxes and later planted out in rows 40 in. apart, with 18 in. between plants, in the experimental field. The most pronounced characteristic of the individuals of this population was their prostrate habit of growth, which at first was thought to be due to the direct effect of the extremely close grazing that the plants had been subjected to in their natural habitat both by rabbits and sheep. At Corstorphine the plants were examined at intervals for a duration of two years, and although the growth was more vigorous than in the natural habitat they still retained their low habit of growth and remarkable uniformity for this and other characters. Several of the plants were transplanted into pots and placed in a greenhouse where hand-crosses were carefully made between similar phenotypes. The progeny arising from a few crosses were not uniform for the flat character, thus indicating that the parents were not all of the same genotype. It is significant that crosses between pairs of similar phenotypes gave in the majority of cases more or less uniform progeny with the prostrate habit of growth.

Since all the individuals collected from the one population showed:

(1) the prostrate habit of growth;

(2) that when they were allowed to develop naturally (at Corstorphine) without grazing or cutting, they retained their characteristic habit of growth;

(3) that they were not all homozygous prostrates;

then selection of some sort had made the population *phenotypically* alike. A possible explanation of this uniformity of phenotype is as follows: Owing to the heavy grazing only certain genotypes which could produce like phenotypes under the particular conditions could survive or at least set seed. This is borne out by the fact that the plants were all phenotypically alike, yet differed in their genetic constitution. It is possible therefore that if the environment can produce from a certain genotype a prostrate phenotype, this genotype will survive in the population. It

does not necessarily follow that these genotypes will produce prostrate plants in all environmental conditions. Certain other characteristics of the genotype of the same population have no doubt influenced the type. When plants of this and of an erect commercial population were compared it was ascertained that the great majority of tillers of the wild

Fig. 1. *Lolium perenne.* Erect and prostrate forms. Photographed in February.

Fig. 2. *Lolium perenne.* Pieces of one prostrate plant grown under different soil conditions. *Left,* sand; *Right,* loam.

population arose from nodes below or at the ground surface, and rarely from nodes above ground, while in the commercial populations a higher proportion of tillers developed from the nodes above the ground level. A difference in the length of internodes was also found. These several

characteristics will undoubtedly aid the preservation of the genotype in areas where grazing is severe.

As regards the origin of this more or less true breeding population the following suggestions are tentatively made:

Starting with a heterozygous population it can be suggested that the suppression of the "erects" by the existing conditions has led to the crossing between only the homozygous "prostrates" and the heterozygous "prostrates" in this highly self-sterile population.

Even if these latter were equally favoured by the environment the population would become pure for prostrateness in a mechanical manner.

If the population were originally homozygous for prostrateness, it is not difficult to see that the heterozygotes may have arisen through stray pollen from other populations.

It is however immaterial for the argument whether the variation originated in the vicinity or was conveyed from a distance. The important point is that if *Lolium perenne* had been unable to produce such a variation, the area in question would have been populated with other species more suited to the prevailing conditions.

Some leaf measurements were made for this population. The following table compares the readings with those taken for another population of perennial ryegrass. The measurements were made in March.

TABLE I.

Leaf Measurements (L. perenne).

Population A				Population B			
Plant No.	Average length of 5 basal leaf blades cm.	Average width of 5 basal leaf blades mm.	Average No. of ribs on 5 basal leaf blades	Plant No.	Average length of 5 basal leaf blades cm.	Average width of 5 basal leaf blades mm.	Average No. of ribs on 5 basal leaf blades
6	9·4	4·6	16·8	1	16·5	4·6	15·8
2	9·7	4·7	17·4	3	16·7	4·5	17·2
5	10·3	4·7	16·2	6	17·3	4·2	15·0
7	10·3	4·4	17·4	2	17·6	4·2	15·0
1	10·8	4·7	18·0	7	17·8	4·6	16·2
4	11·0	4·6	18·4	5	18·5	3·7	13·0
3	11·8	4·3	15·2	4	19·6	3·9	15·4
Average	10·5	4·6	17·1	Average	17·7	4·2	15·4

Both populations were grown under similar conditions for two years at Corstorphine. The length of the leaf is the distinguishing feature between the two.

Plants of another grazed population of *L. perenne* growing in a small

glen 500 ft. above sea-level in East Lothian were also studied at Corstorphine.

This glen has been under the plough at one time but certainly not within the last 60 years. Grazing is severe during the spring and early summer, but late in the season is not so heavy.

The population in its natural habitat appeared to be more or less uniform. This apparent uniformity however was probably the result of modificatory dwarfing of the plants by the extreme environmental conditions. Plants from this population grown at Corstorphine showed themselves to be either (1) prostrate or (2) of a bushy type. It is noteworthy that the erect type commonly found in the commercial strains of *Lolium perenne* was absent.

It is probable that the population was a mixed one sown down by man, since this species does not inhabit the neighbouring glens and hills. It is suggested that the mixture contained genotypes suited to the existing conditions, otherwise the *Agrostis* spp. growing in abundance nearby would long ago have crowded out the perennial ryegrass.

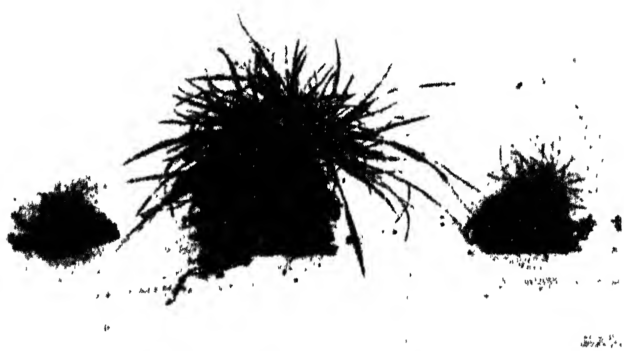

Fig. 3. *Lolium perenne.* Normal plant in centre.

Before considering the next species, *Dactylis glomerata*, it is perhaps necessary to lay further emphasis on the importance of constant severe grazing in producing a typical population of *L. perenne*. In many old pastures in districts where the agricultural requirements do not permit of constant heavy grazing throughout the year, and especially in districts where the number of rabbits is limited, the persistence of *L. perenne* does not necessarily depend on the presence within the population of prostrate perennial types, but rather on the annual re-

seeding of many types. This may possibly explain the reason for some old agricultural pastures containing several forms of perennial ryegrass.

In addition to the influence of animals on the composition of a population there is also severe competition between individual plants. When certain plants from the coastal population were crossed at Corstorphine a few weakly individuals were obtained (Fig. 3). These bred true when intercrossed.

Under natural conditions such plants do not survive, since none were found growing wild. In culture however it was possible to raise them to maturity.

Dactylis glomerata. This Linnaean species was also found to exhibit great variations (cf. Figs. 4 and 5).

Some of the types owe their particular appearance to modifications due to the direct effect of environment, but others are true variations. While possibly there are dwarfs and prostrate plants which owe their characteristic appearance to the effect of habitat, it seems almost certain that there are definite prostrate types apart from the direct effect of environment; it is to be assumed that these latter will withstand heavy grazing better than modificatory dwarfs.

For the experiments with *D. glomerata* plants were collected from a heavily grazed hill population growing 1000 ft. above sea-level in East Lothian. These plants, after a short period of growth in boxes, were planted out in the experimental field at Corstorphine. After one year's growth, under this environment, they were examined and proved to be remarkably uniform as regards habit of growth. In addition to the study of the original plants of this population at Corstorphine, it was thought advisable to raise seedlings from "natural" seed (*i.e.* seeded without isolation) collected from the natural habitat. Small areas on the hill were enclosed by wire netting, in order to prevent grazing and to permit of the development and seeding of the cocksfoot plants. The seed collected was sown at Corstorphine, and the plants raised were found to be more or less true to type, with no evidence of the coarse type so commonly found on road sides. The habit of growth of this type therefore appears to be an inherited variation and not merely a modification of the tall growing form.

Other plants were collected from coastal populations; one lot from the sea braes in Berwickshire, only a few miles distant from the situation occupied by the previously mentioned East Lothian population, and the other from the sea braes in Forfarshire. These sea braes were heavily grazed by rabbits, and in the case of the Berwickshire population by

Fig. 4. *Dactylis glomerata*. Erect and prostrate forms. Photographed in February.

Fig. 5. *Dactylis glomerata*. Broad and narrow-leaved forms. Photographed in February.

sheep as well. Both populations were growing in positions exposed to the sea spray. When they were grown in culture at Corstorphine it was ascertained that certain characteristics such as colour of leaf (bluish-

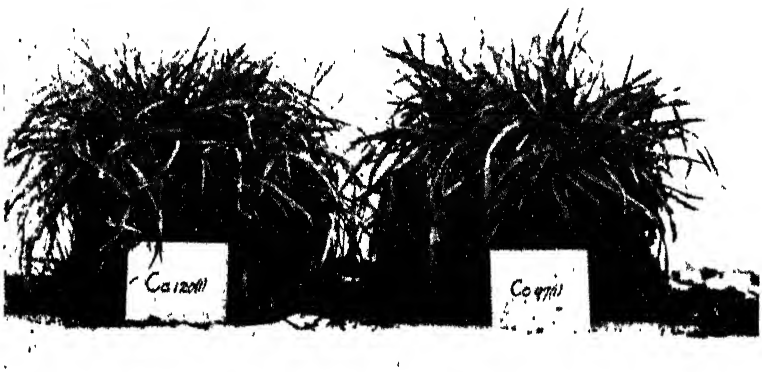

Fig. 6. *Dactylis glomerata.* Plant on left from Berwickshire coast population. Plant on right from East Lothian hill population. Photographed in February.

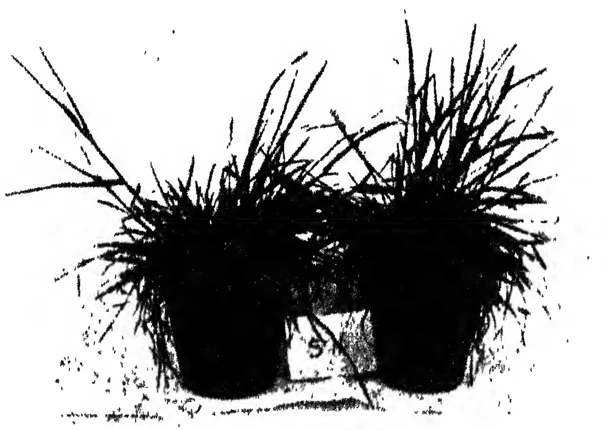

Fig. 7. *Dactylis glomerata.* Two plants from Berwickshire coast population. Photographed in June.

green) and thickness of leaf were merely modifications due to the extreme environment; but the typical habit of growth, although the plants attained larger proportions, remained constant (cf. Fig. 6).

The following rather important facts concerning the two coastal populations are worthy of note:

Fig. 8. *Phleum pratense.* Erect form. Photographed in August.

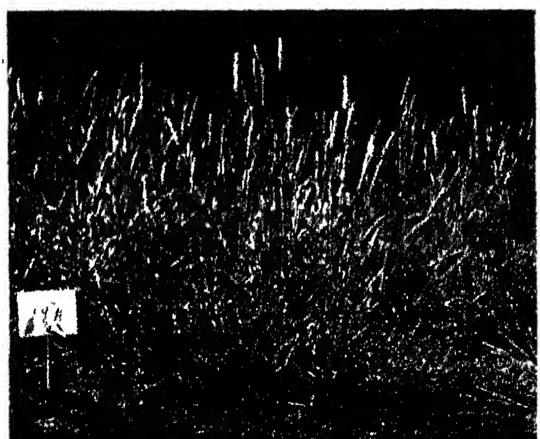

Fig. 9. *Phleum pratense.* Spreading form. Photographed in August.

(1) The individuals within each population resemble each other closely;

(2) The populations themselves are very similar in habit of growth, and

(3) They resemble, in habit of growth, the East Lothian hill population (cf. Fig. 6).

Whether these three populations have in common individuals of like genetic constitution has yet to be determined by experiment, but there is strong evidence that close grazing, among other factors, has acted as a selective agent in leading to uniformity for a definite type or variety.

Two years ago seed was collected from a population growing on the sea braes in Kincardineshire at a place where there was no grazing. The plants raised from this seed are quite distinct from the grazed Berwickshire population as regards habit of growth. This fact strengthens the view that different genotypes assume ecological dominance under different conditions.

With regard to shade forms of cocksfoot, Turesson has made some interesting observations. He concludes that *Dactylis glomerata* var. *lobata* is probably a hereditary shade variety and not a modification due to direct effect of environment; although undoubtedly certain characteristics ascribed to the form are the result of extreme environment, as for instance the great looseness of the tuft and the pure green colour of the leaves and panicles, all of which characters disappear in culture.

Phleum pratense. It is probable that *P. pratense* also has distinct hereditary habitat types (cf. Figs. 8 and 9). But with this species much greater difficulty was experienced in obtaining wild material in Scotland. So far it has been possible to collect only four plants from a habitat which has never been under the plough. These four plants were taken from a heavily grazed glen in East Lothian and are almost identical in appearance. They are of a low growing, rather fine-leaved type (cf. Fig. 9).

Phleum alpinum. The species *P. alpinum* is of particular interest as its distribution is very limited in Britain. There is a distinct gap between the lower limits of distribution of *P. alpinum* and the upper limits of *P. pratense*, therefore there is little chance of crossing occurring between the two species.

Material of *P. alpinum* was removed from an isolated population growing in Aberdeenshire. The individuals of this population were found to be self-fertile and set seed freely when tested at the Plant Breeding Station. But in 1923 no seeds were obtained from many ripe

panicles gathered from the natural habitat. Whether the usual method of reproduction is vegetative, with sexual reproduction occurring only during favourable seasons, we do not know. However, the plants collected show little variation; and several hundred selfed seedlings, which have been grown from them, are uniform in the seedling stage (cf. Fig. 10).

Crosses between *P. alpinum* and *P. pratense* have been made with a view to increase the variability of *P. alpinum*, and afford material for subsequent study of types suited to a wider range of conditions. As the usual method of crossing grass flowers failed to give results, owing to

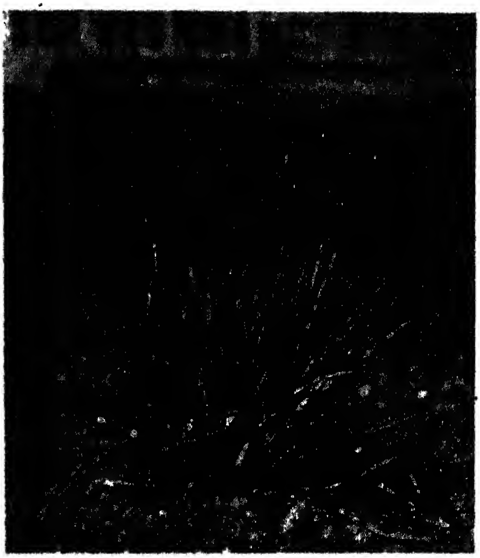

Fig. 10. *Phleum alpinum*. Grown in culture. Age 7 months.

the "drying out" of the panicle due to the necessary removal of a considerable number of flowers before emasculation was possible, the following method has been employed with some success. The anthers of *P. alpinum* were removed after the flowers had opened but before dehiscence of the anthers had taken place. Pollen of *P. pratense* was applied to the stigmas, after which the entire panicle was enclosed in a pergamine bag. This method has many disadvantages from the experimental point of view as occasional flowers opened, and shed pollen, after the maximum daily flowering period was over. Probably a better method would be that of applying the *P. alpinum* pollen to a self-sterile plant of *P. pratense*. However, there is little doubt that several crosses have been obtained, but the plants are still in the seedling stage.

If such crosses had taken place in nature, an improbable occurrence in view of the present distribution of the two species, it is possible that a greater number of genotypes of *P. alpinum* would have been the result, and therefore a more extended range of distribution. If it be proved that these isolated populations of *P. alpinum* have become more or less constant in genotype the species has lost an important method of attaining increased variability—that of hybridisation with plants of another genetic constitution.

In conclusion it is necessary to add a few remarks on the economic value of this line of research. At the present time the commercial strains of our agricultural grasses such as *L. perenne*, *D. glomerata* and *Phleum* spp. are not well suited to pasture purposes, although they are admirable as seed producers and as hay grasses. There seems little doubt that this state of affairs has resulted from the continual selection, both natural and artificial, of the heavy seeding early maturing types. It is, however, believed by some that this condition has been brought about by the inheritance of characters which have been acquired—not selected —by the treatment received under agricultural conditions. If such a theory is held it would only be a matter of time before any "wild" pasture type deteriorated. But if one assumes that the cultivated type has resulted from the constant selection of the heavy seeding, early maturing genotypes within the species, it should be possible to raise strains of pasture grasses which would in no way deteriorate so long as the pasture genotypes remained in the strain. Moreover, by the study of the problem of the hereditary variation of wild plants in relation to habitat the obtaining of material for breeding work is simplified. It is by the study of populations that have undergone a process of natural selection, that a start may be made with strains which have attained a certain uniformity and are suited to various environmental conditions.

Summary.

These few observations on the different species of grasses named suggest several important conclusions, viz.:

(1) That there exist definite hereditary habitat types within the grass species.

(2) That the habitat type represents the genotypical response of the species-population to a definite habitat; and that habitat types have not necessarily arisen through chance isolation of variations, or by a gradual change from one type to another without selection of individuals. In this connection Nägeli, Bateson, and Turesson have pointed

out that the intermediate area between two habitats is not populated by a uniform type but by a mixture of the two types existing in the adjoining habitats.

(3) That, as there was phenotypic uniformity and not complete genotypic similarity in the coastal population of perennial ryegrass, there have been two processes of selection in progress, (*a*) phenotype selection and (*b*) genotype selection.

(4) That without doubt extreme environmental conditions (*e.g.* strong salt-laden winds) alter the appearance of plants; should the effect of such conditions, however, be merely modificatory and not selective, the inherited properties of the population will remain unchanged, although the appearance of the plants has changed. It is, however, possible that some genotypes may be more influenced by the direct effect of the environment than others. Therefore it can be seen that although a population may be phenotypically uniform, it is possible that the various genotypes forming this population may differ in their reaction to other environments.

(5) That the conditions of the environment (other than direct competition among related species and races) are by no means unimportant. Under this head come the effects of high winds, animal and human activity etc. which factors are, as selective agents, of very considerable importance in leading to the establishment of a definite type or variety. In this connection the results of the experiments bear out the statement made by Smith that "the protection of the buds is fundamental as regards the biological factors."

(6) The species *L. perenne*, *D. glomerata* and *P. pratense* have similar prostrate forms.

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